AUSTRALIAN JOURNAL OF ZOOLOGY

VOLUME 3
NUMBER 3
OCTOBER 1955

REGISTERED IN AUSTRALIA FOR TRANSMISSION BY POST AS A PERIODICAL

AUSTRALIAN JOURNAL OF ZOOLOGY

Published by the Commonwealth Scientific and Industrial Research Organization, in collaboration with the Australian National Research Council, and under the general direction of the Editorial Board (Dr. N. S. Noble (Chairman), Professor J. S. Anderson, Professor Sir Macfarlane Burnet, Professor L. H. Martin, and Professor J. G. Wood). A medium for the publication of results of original scientific research in zoology with special emphasis on the descriptive phases

Issued as material becomes available, 7/6 per issue

EDITORIAL ADVISORY COMMITTEE

OTHER JOURNALS PUBLISHED BY C.S.I.R.O.

Australian Journal of Physics Australian Journal of Chemistry Australian Journal of Biological Sciences Australian Journal of Applied Science	Issued quarterly, 30/- per annum
Australian Journal of Agricultural Research	Issued six times a year, 30/- per annum
Australian Journal of Marine and Freshwater Research Australian Journal of Botany	Not issued at regular intervals, 7/6 per issue

The Organization is a signatory to the Fair Copying Declaration, details of which may be obtained from the office of the Royal Society, London.

All enquiries and manuscripts should be forwarded to:

The Editor,
Australian Journal of Zoology,
Commonwealth Scientific and Industrial Research Organization,
314 Albert Street, East Melbourne, C.2, Victoria

MELBOURNE

NOTE ON THE MATHEMATICAL THEORY OF POPULATION DYNAMICS AND A RECENT FALLACY

By J. R. PHILIP*

(*Manuscript received July* 16, 1954)

Summary

Principles are outlined for the construction of a consistent theoretical treatment of the various problems of population dynamics.

Three types of interspecific competition are distinguished, "imperfect", "perfect", and "hyperperfect", depending on whether the product $\alpha\beta$ in the Lotka-Volterra equations is less than, equal to, or greater than unity. It is shown that perfect competition, which is of especial relevance to the problems of natural selection and evolution, leads to a much simpler set of inequalities and limits than those commonly quoted as resulting from the Lotka-Volterra equations. It is shown that in perfect competition the surviving species is not necessarily superior in "reproductive efficiency". "Metabolic efficiency" is equally important.

This restatement of the problems of population dynamics is used to demonstrate the falsity of the recent claim of Andrewartha and Birch (1953) that a fundamental contradiction exists in the Lotka-Volterra equations for interspecific competition.

I. INTRODUCTION

The present confusions in the theory of population dynamics (many of which have been discussed by Smith (1952)) arise largely from the application of equations to irrelevant situations and from the lack of a consistent basis for the study of distinct but related problems. The present paper is concerned with general principles, their application to the problem of interspecific competition, and a discussion of the fallacious treatment of the Lotka-Volterra theory of interspecific competition put forward by Andrewartha and Birch (1953).

It is emphasized that the theoretical framework developed here is the simplest possible, and depends on the assumption that each individual of the species is equivalent to any other, no account being taken of the age or sex distribution of the population. Furthermore, the theory is deterministic rather than stochastic. Extensions of the theory are possible in principle, which take account of the variability of the demographic parameters both with age and sex and in a random manner in time.

These refinements will be avoided in the present paper, which is intended to clarify ideas rather than to erect a completely general theoretical edifice.

* Regional Pastoral Laboratory, C.S.I.R.O., Deniliquin, N.S.W.

II. Basic Equation of Population Growth of Single Species

The basic equation describing the rate of change of the population density of a single species is

$$(1/N)\,(\mathrm{d}N/\mathrm{d}t) = b - d - s/1\delta_i, \quad \ldots\ldots\ldots \quad (1)$$

where N is the density of population at time t, b and d are the birth and death rates respectively in an "unlimited environment", and

$$\delta_i = \Delta_i b + \Delta_i d,$$

where $\Delta_i b$ is the decrease in birth rate due to limiting factor i, and $\Delta_i d$ is the increase in the death rate due to limiting factor i.

No attempt will be made to enumerate the s limiting factors. Note that b, d, and all Δb's, Δd's, and δ's are expressed as births or deaths per individual per unit time.

Any particular problem of population dynamics involving a species is then reduced to expressing the δ's for each of the species as functions of the environment and (where relevant) the population densities of the a species. In this manner a equations will be constructed involving a unknowns. These equations, together with the initial conditions, will in general enable a determinate solution. Only in simple cases will solutions be available by analytic means; but numerical methods will enable the solution of specific instances for the most complicated system of equations.

Basically, then, the problems of population dynamics reduce to establishment of the forms of the δ-functions. Once the forms of the relevant δ-functions are fixed, a consistent framework can be constructed which will embrace such phenomena as interspecific competition, parasitism and predation in renewed, unrenewed, or periodically fluctuating environments.

III. Simple Case of Density-Dependent Factor

Consider the simple case of the population density of a single species in which the single limiting factor is density-dependent. Without loss of generality, we may regard this factor as food supply, realizing that the same argument will hold should the factor be another density-dependent one such as water-supply or living-space.

Then in equation (1), let suffix 1 refer to food supply and let

$$r = b - d.$$

Since food supply is the single limiting factor,

$$\sum_{2}^{s} \delta_i = 0;$$

so that

$$(1/N)\,(\mathrm{d}N/\mathrm{d}t) = r - \delta_1. \quad \ldots\ldots\ldots\ldots \quad (2)$$

Let F be the quantity of food available to the species per unit time. Then δ_1 is obviously a function of F/N, the mean rate at which food is available per head of population. When

$$F/N = 0, \quad \delta_1 \to \infty,$$

since the population cannot exist without food. When N is small and F/N is large, the limit of food supply exercises little influence on population

growth and δ_1 is negligibly small. The simplest function available to describe such a relationship is the reciprocal, which is adopted here.

Thus

$$\delta_1 = N/\mu F, \quad \ldots\ldots\ldots\ldots\ldots \quad (3)$$

where μ is a constant, expressing the sensitivity of the species to food shortage. μ is small for a species which suffers a marked population check under conditions of low food supply, and is large for one less sensitive to such conditions. μ can, in fact, for a given size of individual, be regarded as an index of the efficiency of metabolism of the species.

Then use of **(3)** in **(2)** gives

$$(1/N)\,(dN/dt) = r - N/\mu F, \quad \ldots\ldots\ldots \quad (4)$$

or

$$dN/dt = Nr(1 - N/K), \quad \ldots\ldots\ldots\ldots \quad (5)$$

where

K r

CORRIGENDA

VOLUME 3, NUMBER 3

Page 288: Equation **(1)** should read:

$$(1/N)\,(dN/dt) = b - d - \sum_{1}^{s}\delta_i, \quad \ldots\ldots\ldots \quad (1)$$

Page 295: The title should read:

STUDIES ON THE NON-PARASITIC STAGES OF THE CATTLE TICK, *BOOPHILUS MICROPLUS* (CANESTRINI) (ACARINA: IXODIDAE)

Then equations similar to **(4)** can be written for each species

$$(1/N_1)\,(dN_1/dt) = r_1 - (N_1 + \alpha N_2)/\mu_1 F, \quad \ldots\ldots \quad (8)$$

$$(1/N_2)\,(dN_2/dt) = r_2 - (\beta N_1 + N_2)/\mu_2 F, \quad \ldots\ldots \quad (9)$$

where an individual of species 2 has α times the depressing effect on the rate of increase of N_1 that an individual of species 1 has; and an individual of species 1 has β times the depressing effect on the rate of increase of N_2 that an individual of species 2 has.

Consider the situation in which competition between species is due simply to the diminution in the food supply of each species by the quantity eaten by its competitor, the food of each species being of identical composition. Then if each member of species 1 consumes θ_1 (and each member

of species 2 consumes θ_2) units of food per unit time, we have from equations (8) and (9),

$$(N_1 + \alpha N_2)\theta_1 = N_1\theta_1 + N_2\theta_2, \quad \ldots\ldots\ldots \quad (10)$$

$$(\beta N_1 + N_2)\theta_2 = N_1\theta_1 + N_2\theta_2, \quad \ldots\ldots\ldots \quad (11)$$

whence

$$\alpha = \theta_2/\theta_1, \quad \beta = \theta_1/\theta_2, \quad \text{and} \quad \alpha\beta = 1.$$

By analogy with the terminology of economics in which competition between firms producing identical goods is termed "perfect" (Robinson 1933), it is suggested that this form of interspecific competition in which $\alpha\beta = 1$ be called "perfect interspecific competition".

Two other types of interspecific competition are possible. Firstly, it may happen that the "ecological niches" of the two species are not identical but overlap to some degree. In this case, either α or β or both are less than if perfect competition were in operation. Clearly, $\alpha\beta < 1$ for this form of competition, for which the term "imperfect interspecific competition" is suggested. The analogy with the imperfect competition of economics (Robinson 1933) is again obvious.

Secondly, the consumption of food by one or both species may be inhibited by the physical presence of the other species, or odours, or excreta exuded by the other species. In this case, the depressing effect of its competitor on the population growth of one or both species is greater than for perfect competition. Obviously $\alpha\beta > 1$ for this type of competition, which we shall designate "hyperperfect interspecific competition".

The oft-quoted criteria which determine the equilibrium values of N_1 and N_2 as $t \to \infty$ (Lotka 1925, 1932; Volterra 1926, 1931; Gause and Witt 1935; Crombie 1945; Hutchinson and Deevey 1949; Andrewartha and Birch 1953) can now be rewritten in the following simpler form for perfect competition. Some simplifications also occur for imperfect and hyperperfect competition, but these will not be discussed here.

V. Equilibrium under Perfect Competition

Because $\alpha\beta = 1$, the conditions reduce to:

Case (*a*) : If $\mu_1 r_1/\alpha > \mu_2 r_2$,

$$\lim_{t \to \infty} N_1 = \mu_1 r_1 F, \qquad \lim_{t \to \infty} N_2 = 0.$$

Case (*b*) : If $\mu_1 r_1/\alpha < \mu_2 r_2$,

$$\lim_{t \to \infty} N_1 = 0, \qquad \lim_{t \to \infty} N_2 = \mu_2 r_2 F.$$

Case (*c*) : If $\mu_1 r_1/\alpha = \mu_2 r_2$,

$$(N_1 + \alpha N_2)/\mu_1 F r_1 = (\beta N_1 + N_2)/\mu_2 F r_2.$$

Whence, from (8) and (9)

$$dN_1/dN_2 = N_1 r_1/N_2 r_2.$$

Integrating and using the initial conditions $N_1 = n_1$, $N_2 = n_2$, at $t = 0$, we obtain

$$(N_1/n_1)^{r_2} = (N_2/n_2)^{r_1},$$

or

$$N_2 = n_2(N_1/n_1)^{r_2/r_1}, \quad \ldots\ldots\ldots\ldots\ldots\ldots (12)$$

also for $t \to \infty$

$$N_1 + \alpha N_2 = \mu_1 r_1 F. \quad \ldots\ldots\ldots\ldots\ldots\ldots (13)$$

Equations (12) and (13) may be solved to give values of $\lim_{t \to \infty} N_1$ and $\lim_{t \to \infty} N_2$. The limiting values will depend on the initial densities n_1 and n_2, and the ratio r_2/r_1. They will always be finite, lying between 0 and $\mu_1 r_1 F$ and 0 and $\mu_2 r_2 F$ respectively.

VI. Perfect Competition as an Agent of Natural Selection

Application of population dynamics studies to problems of natural selection and evolution is of the greatest biological interest. A very simple but important problem deals with the operation of natural selection between two closely related species (or even phenotypes) occupying the same ecological niche.

For this situation perfect competition obviously holds. (The reader is reminded that the present treatment takes no specific account of differential liability to predation or parasitism of the two species.) Further, if the rate of feeding of individuals of each species (or phenotype) may be taken as equal, $\alpha = \beta = 1$ and the conditions given above become even simpler.

The quantities $\mu_1 r_1/\alpha$, $\mu_2 r_2$ appearing in these conditions represent the products of relative measures of the efficiency of reproduction and of metabolism of the species. Interpreting the theory in this light it is seen that the species possessing the greater combined efficiency of reproduction and metabolism is the survivor and that the less efficient species ultimately becomes extinct.

Case (*c*), in which any advantage in fertility of the one species is offset by the greater metabolic efficiency of the other, is trivial. Any such equilibrium would be highly unstable, and the smallest changes in μ or r would result in the extinction of one species and the full occupancy of the niche by the survivor.

VII. The Andrewartha-Birch Fallacy

A fallacy occurs in a recent paper of Andrewartha and Birch (1953). We shall ignore here some relatively minor inadequacies of their treatment and consider only the keystone of their argument.

This is their rejection, as absurd, of the possibility that for some finite value of t, T either

$$\left.\begin{aligned} K_1 &< N_1 + \alpha N_2 \\ K_2 &< \beta N_1 + N_2 \end{aligned}\right\}, \quad \ldots\ldots\ldots\ldots\ldots\ldots (14)$$

or

where, in the notation adopted above

$$\left.\begin{aligned} K_1 &= \mu_1 r_1 F \\ K_2 &= \mu_2 r_2 F \end{aligned}\right\}. \quad \ldots\ldots\ldots\ldots\ldots\ldots (15)$$

Certainly, it would be absurd to suggest that these inequalities should hold *at equilibrium*, but this is in no circumstance implied by the Lotka-Volterra equations.

This point will be clearer if we translate **(14)** into the terms we have introduced earlier in this communication. Then **(14)** becomes for some finite value of t, T either

$$\left.\begin{aligned} &F/(N_1 + \alpha N_2) < 1/\mu_1 r_1 \\ \text{or} \\ &F/(\beta N_1 + N_2) < 1/\mu_2 r_2 \end{aligned}\right\} \quad \ldots\ldots\ldots\ldots \quad \textbf{(16)}$$

The verbal equivalent of **(16)** is for some finite value of t, T, either

$$\left.\begin{aligned} &\text{the food supply of species 1 becomes} \\ &\text{less than } 1/\mu_1 r_1 \text{ units per head,} \\ \text{or} \\ &\text{the food supply of species 2 becomes} \\ &\text{less than } 1/\mu_2 r_2 \text{ units per head.} \end{aligned}\right\} \quad \ldots\ldots\ldots\ldots \quad \textbf{(17)}$$

If the initial populations of 1 and 2 are both small, the food supply per head of each population will be high and both populations will increase. As population increase continues, the level of food supply per head will obviously diminish in each case, until one or other of the inequalities in **(16)** holds. To fix ideas, let us suppose it is the second inequality which becomes true. Then, obviously, from that point on species 2 declines in numbers, but species 1 is free to increase so long as its food supply per head stays in excess of $1/\mu_1 r_1$. The increase in N_1 and decrease in N_2 continues until equilibrium is attained at which

$$\lim_{t \to \infty} N_1 = \mu_1 r_1 F \quad \text{and} \quad \lim_{t \to \infty} N_2 = 0.$$

Figure 1 shows this process graphically for a simple numerical example of perfect competition. Similar figures may be drawn to represent imperfect and hyperperfect competition, though their interpretation is somewhat more complicated.

The process described above is certainly not absurd, and can be in good agreement with observation (e.g. Utida 1953).

The biological significance of the theory rests on this very point that species 1 has the capacity to continue to increase at a time when the numbers of species 2 begin to decline because of the low level of food supply per head. Species 2 is, in fact, "starved out", when food is the density-dependent factor. Similarly, if space were the factor, the species would be, literally, crowded out.

Andrewartha and Birch having, to their satisfaction, demonstrated that the work of Lotka and Volterra on interspecific competition is nonsensical, reach "the *general* conclusion that these mathematical models—are more likely to confuse than help in the interpretation of observations and measurements of natural populations".*

* Italics are the present authors.

It is a fact that certain equations which have been put forward to describe population changes are obviously erroneous (*vide* remarks above concerning the Gompertz equation), but even had Andrewartha and Birch been able to choose from the literature one which was blatantly in error,

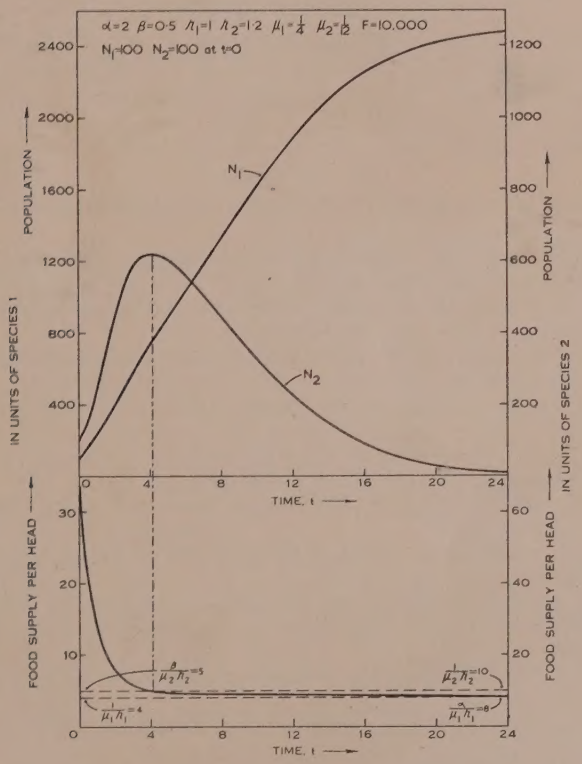


Fig. 1.—Interspecific perfect competition resulting in the extinction of species 2. The higher fertility of species 2 is insufficient to offset the greater tolerance of species 1 to low levels of food supply. The decline of food supply per head is shown in the lower part of the figure. Note that N_2 begins to decrease as soon as the food supply per head of species 2 falls below $1/\mu_2 r_2$.

no demolition of this equation, however competent, could possibly justify their sweeping conclusion. The *non sequitur* with which they terminate their paper is a more dangerous fallacy than the one we have exposed above.

It need hardly be stressed that it is equally dangerous to use mathematical models uncritically. The essential purpose of setting up these

models is to explore the implications of the initial assumptions and, naturally, the adequacy of the model depends on that of the assumptions. The reader is referred to Moran (1954) for a useful discussion of the role of mathematical models in population studies.

VIII. Acknowledgments

The author wishes to thank Professor P. A. P. Moran, National University, Canberra, A.C.T., and Dr. E. J. Williams, Division of Mathematical Statistics, C.S.I.R.O., for stimulating discussion of these matters.

IX. References

Andrewartha, H. G., and Birch, L. C. (1953).—The Lotka-Volterra theory of interspecific competition. *Aust. J. Zool.* 1: 174.

Crombie, A. C. (1945).—On competition between different species of graminivorous insects. *Proc. Roy. Soc.* B 132: 362.

Gause, G. F., and Witt, A. A. (1935).—Behaviour of mixed populations and the problem of natural selections. *Amer. Nat.* 69: 596.

Hutchinson, G. E., and Deevey, E. S. (1949).—Ecological studies of populations. *Surv. Biol. Progr.* 1: 325.

Lotka, A. J. (1925).—"Elements of Physical Biology." (Williams & Wilkins: Baltimore.)

Lotka, A. J. (1932).—The growth of mixed populations: two species competing for a common food supply. *J. Wash. Acad. Sci.* 22: 461.

Moran, P. A. P. (1954).—The logic of the mathematical theory of animal populations. *J. Wildlife Mgmt.* 18: 60.

Nicholson, A. J. (1954).—An outline of the dynamics of animal populations. *Aust. J. Zool.* 2: 9.

Pearl, R., and Reed, L. J. (1920).—On the rate of growth of the population of the United States since 1790 and its mathematical representation. *Proc. Nat. Acad. Sci. Wash.* 6: 275.

Smith, F. E. (1952).—Experimental methods in population dynamics, a critique. *Ecology* 33: 441.

Robinson, Joan (1933).—"The Economics of Imperfect Competition." (Macmillan & Co.: London.)

Utida, S. (1953).—Interspecific competition between two species of bean weevil. *Ecology* 34: 301.

Verhulst, P. F. (1838).—Notice sur la loi que la population suit dans son accroissement. *Corr. Math. et Phys.* 10: 113.

Volterra, V. (1926).—Variazioni e flutuazioni del numero d' indivui in specie animali conviventi. *Mem. Accad. Lincei* 2: 31.

Volterra, V. (1931).—"Leçons sur la Théorie Mathematique de la Lutte pour la Vie." Cahiers Scientifiques No. 7. (Gauthiers-Villars: Paris.)

Wilson, E. B. (1934).—Mathematics of growth. *Cold Spr. Harb. Symp. Quant. Biol.* 2: 199.

Addendum

The use and misuse of mathematics in population studies and the limitations of the Lotka-Volterra equations receive excellent treatment in Nicholson (1954) which appeared after the communication of the present paper.

STUDIES OF THE NON-PARASITIC STAGES ON THE CATTLE TICK, *BOOPHILUS MICROPLUS* (CANESTRINI) (ACARINA: IXODIDAE)

By The Late L. F. Hitchcock*

(*Manuscript received December* 31, 1954)

Summary

Laboratory studies of the effects of temperature and relative humidity on the non-parasitic stages of the cattle tick, *Boophilus microplus* (Canestrini),† are described.

The pre-oviposition period ranged from 19-39 days at 59-60°F to 2-3 days at 97°F.

The duration of oviposition was uninfluenced by relative humidity but varied from a maximum of 44 days at 59°F to a minimum of 4 days at 102°F. The minima at each temperature were exceedingly irregular, due to the deaths of ticks.

The number of eggs laid by a female tick was uninfluenced by relative humidity. The peak oviposition mean of 2496 eggs per female occurred at 75°F, fewer eggs being laid at higher and lower temperatures. Daily egg output attained a maximum of 197 at 92°F, but was uninfluenced by relative humidity.

The water loss of engorged female ticks was greatly affected by inert dusts and even dusting with a sample of soil chosen at random produced a significant increase in water loss.

Developmental period was uninfluenced by order of deposition, but percentage hatch of eggs laid during the last few days of oviposition is lower. Eggs did not hatch at constant relative humidities lower than 70 per cent., but some were able to survive relative humidities lower than this if exposed periodically to a saturated atmosphere. The period of development of eggs varied from a maximum of 146 days at 62°F to a minimum of 14 days at 97°F. Maximum hatch occurred between 85 and 95°F, and at relative humidities above 95 per cent. Exposure of eggs to temperatures below the developmental zero prolonged the period of development merely by the period of exposure. Regular alternation of temperature between the limiting temperatures of 59 and 97°F with a steady rise or fall between the extremes resulted in development at a rate approximately equal to that obtained at constant temperature of 78°F, the arithmetic mean of the above figures.

Larval longevity was influenced markedly by temperature and humidity. A maximum of 240 days was recorded at 72°F and 90 per cent. relative humidity. Larvae are able to recoup water losses sustained at low relative humidity by absorption from the atmosphere during subsequent periods of high relative humidity.

* Formerly of Division of Entomology, C.S.I.R.O., Veterinary Parasitology Laboratory, Yeerongpilly, Qld. This paper was completed by Mr. K. R. Norris and Mr. G. J. Snowball, Division of Entomology, from a first draft prepared by the author before his death in May 1953.

† The author has followed the nomenclature of Cooley (1946).

I. Introduction

A study was undertaken of the effects of temperature and humidity on the non-parasitic stages of *Boophilus microplus* (Canestrini) which comprise the engorged female, the egg, and the larva. During this work, the results of which are presented in the present paper, most attention was paid to the extremes of the developmental and survival periods, which are relevant in eradication programmes.

Studies of the biology of the cattle tick in Australia have previously been published by Pound (1899) and Legg (1930). The present study in manuscript was referred to by Seddon (1951). Information on the biology of this species in India has been published by Sapre (1940), and in South America by Gelormini (1940), Boero and D'Angelo (1947), and Ault (1948).

II. Methods

Initially ticks required for cultures and experiments were collected from abattoirs and farms, but later, a culture established on stalled cattle in the laboratory grounds yielded a more reliable supply of ticks of known history.

Experimental material (engorged females, eggs, or larvae) was placed in vials, or pieces of glass tubing. The relative humidity of the atmosphere in which the material was maintained was controlled by the use of saturated solutions of certain salts, or sulphuric acid of various specific gravities. Controlled temperatures were provided by two cabinets which could be operated above or below room temperature. At one stage four small incubators fitted with fans, heaters, and thermostats were operated inside a constant temperature cabinet. Eight different relative humidities were maintained inside each small cabinet, so that with the cabinets operating at four temperatures, 32 combinations of temperature and relative humidity were available at the one time.

III. Influence of Environmental Conditions on the Non-Parasitic Stages of the Cattle Tick

(*a*) *Adult Female*

(i) *Duration of Pre-Oviposition Period.*—In nature, the fully engorged female tick drops from the host and crawls, in response to a negative phototaxis, to a sheltered place. The interval between the fall of the tick and the commencement of oviposition (pre-oviposition period) is influenced by temperature (Table 1). Within the range tested (45-99 per cent.), relative humidity had no influence on the duration of the pre-oviposition period.

Previous studies of the pre-oviposition period of *B. microplus* have been carried out by Legg (1930) in Australia, Gelormini (1940) in Argentina, and Sapre (1940) in India. Legg's studies were not carried out under conditions of controlled temperatures. His "summer" minimum of 2 days agrees with the minimum obtained in the present study at 97°F. Legg's maximum period of 12 days as against the maximum of 39 days

recorded in Table 1 at 59-60°F reflects the very mild winter conditions prevailing at his research centre, Townsville. Gelormini also apparently worked with fluctuating temperatures and his maximum pre-oviposition

TABLE 1

EFFECT OF TEMPERATURE ON THE PRE-OVIPOSITION PERIOD OF B. MICROPLUS

Temperature (°F)	Range of Pre-Oviposition Period (days)*
59-60	19-39
64	10-21
68	6-9
75	3-5
81	2-4
90	2-3
97	2-3

* Based on a minimum of 20 ticks per temperature. Interval between observations one day.

period of 44 days was obtained under temperatures ranging between 32 and 77°F. Therefore, it appears certain that development was completely arrested for periods during this experiment, so that a true developmental period is not indicated. Sapre found a mean pre-oviposition period of 4 days at 71.6°F.

TABLE 2*

EFFECTS OF TEMPERATURE AND RELATIVE HUMIDITY ON NUMBERS OF EGGS LAID BY FEMALES OF B. MICROPLUS†

Temperature (°F)	Mean Numbers of Eggs Laid at Relative Humidity:									Mean
	45%	50%	60%	70%	75%	80%	90%	95%	99%	
59	412		215	198		877	109	739	716	457
64	1729		1939	1408	1770	1470	2070	1760		1718
68	1934			2536		1943	2122	2349	1955	2144
70	1516		1792	2653		2343	2660	2129	1489	2006
75	2667	2398	2613	2133		2497	2163		2663	2519
80		2036	2455	2306	2442	2592			2330	2332
86	1726				1981				1948	1885
92	1828				1745				1960	1844
97	1475				1449				1756	1560
102	1167				1215				905	1101

* Based on a minimum of four ticks per treatment.

† Blank spaces in this and succeeding tables indicate that no test was made at those particular combinations of temperature and humidity.

(ii) *Number of Eggs Laid, Duration of Oviposition, and Daily Egg Output.*—The effects of temperature and relative humidity on the total numbers of eggs laid are illustrated in Table 2. Temperature had a marked

effect on the numbers of eggs laid. Maximum numbers were produced at 75-80°F. At the temperatures tested, lowest egg production was at 59°F. Statistical analysis showed that the effect of temperature on egg production was highly significant, but relative humidity had no effect upon the numbers of eggs laid. The influence of temperature on number of eggs laid has been overlooked by previous authors.

Females did not oviposit when kept at 40°F, but oviposition ultimately commenced when they were transferred to a favourable temperature. Ovipositing females transferred from 84 to 40°F ceased to lay, but resumed after 25 days at 40°F when transferred to the higher temperature once again.

The extremes of the duration of oviposition recorded at various temperatures and humidities are presented in Table 3. According to Legg

TABLE 3

EFFECT OF TEMPERATURE AND RELATIVE HUMIDITY ON THE DURATION OF OVIPOSITION OF B. MICROPLUS*

Temperature (°F)	Range of Egg-Deposition Period in Days at Relative Humidity:								
	40%	45%	50%	60%	70%	75%	80%	90%	99%
40					No eggs	No eggs	No eggs		
59		5-39		18-32	5-35		16-44	23-25	28-42
64		13-26		10-34	27-32		16-39	22-42	25-30
68	17-19	17-19		20-23	17-29		16-39	20-26	19-27
70	14-25	9-15		20-23	23-24		27-31	19-24	16-18
75	13-14	14-15	11-15	15-17	16-22		16-26	17-18	17-18
80			11-12	12-14	13-14		13-16	11-14	12-14
86		7-10			9-12		12-13		9-12
92		8-10				8-9			8-12
97		7-9				8-10			8-12
102		7-10				6-11			4-12

* Based on a minimum of four ticks per treatment.

(1930) the duration of oviposition varied from a summer minimum of 5 days to a winter maximum of 30 days. Once again the mildness of the Townsville winter is reflected, because periods of up to 44 days were recorded at a temperature of 59°F in the present study. Sapre (1940) reports a figure of 18 days at 71.6°F which is well within the range indicated in Table 3. Gelormini (1940) also records a maximum oviposition period of 40 days, but as indicated in a previous section it seems likely that some of his tests were carried out under temperatures which fell low enough at times to inhibit all development.

The mean daily egg output of females of *B. microplus* (i.e. total eggs laid, divided by number of days over which they were laid) was strongly affected by temperature, but no significant effect was produced by the

relative humidity of the cultures (Table 4). This is at variance with the finding of Arthur (1951) that the daily egg output of *Ixodes hexagonus* Leach varied directly with relative humidity.

TABLE 4

EFFECT OF TEMPERATURE AND RELATIVE HUMIDITY ON THE MEAN DAILY EGG OUTPUT OF B. MICROPLUS*

Temperature (°F)	Mean Daily Egg Output at Relative Humidity:								
	45%	50%	60%	70%	75%	80%	90%	95%	99%
59	15.3		7.3	7.0		23.0	4.5	20.0	17.5
64	44.5		46.9	48.6	24.6	54.0	73.8	59.3	
68	107.8			113.0		68.0		98.2	86.8
70	137.0		82.3	106.2		113.3	105.3	95.2	86.8
75	187.3	185.3	161.5	116.0		171.5	154.0		153.2
80		178.0	190.0	117.0	206.0	212.0	172.3		173.2
86	189.6				183.9				193.8
92	202.3				196.4				197.3
97	174.0				161.4				175.5
102	134.6				128.9				94.0

* Based on a minimum of four ticks per treatment.

(iii) *Variation in Rate of Egg Deposition Throughout Period of Oviposition.*—The number of eggs deposited per day is not equal throughout the period of deposition, even at constant temperatures. The daily output rises to a peak shortly after the commencement of oviposition, and

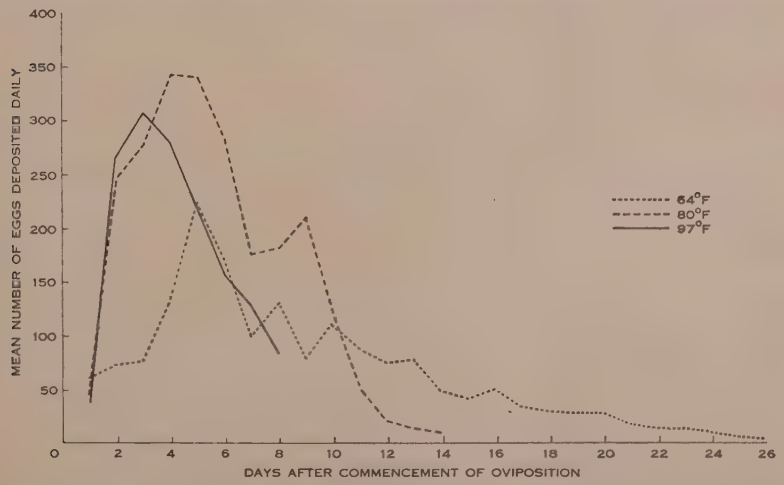


Fig. 1.—Mean daily oviposition by the cattle tick at three constant temperatures.

falls to a low figure towards the end of oviposition (Fig. 1). Gelormini (1940) also observed that egg production reached a peak a few days after the commencement of oviposition.

(iv) *Factors Influencing Longevity of Female Ticks.*—The minimum temperature survived by female ticks has not been determined but, as indicated above, they are able to withstand considerable periods of exposure to temperatures which inhibit all development and activity. In the field on one occasion, a small percentage of female ticks under observation survived in a sward when grass temperatures fell to 20°F on eight successive mornings, and some subsequently laid eggs.

TABLE 5

EFFECT OF INERT DUSTS AND A SOIL SAMPLE ON THE WEIGHT LOSS OF MATURE FEMALES OF B. MICROPLUS* AT 86°F AND VARIOUS RELATIVE HUMIDITIES

R.H. (%)	Treatment	Per Cent. Weight Loss after:						Females Commencing Oviposition on 3rd Day (%)
		1 Day	2 Days	3 Days	4 Days	5 Days	7 Days	
40	Alumina 1†	25	42	Dead				0
	Silica‡	25	42	Dead				0
	Alumina 2§	17	28	29	Dead			0
	Soil	3	6	9	12	16	23	100
	Control	2	4	6	9	12	18	100
50	Alumina 1	22	39	40	Dead			0
	Silica	15	29	34	35	Dead		0
	Alumina 2	13	22	28	33	36	37	20
	Soil	3	5	8	11	13	19	100
	Control	2	4	6	9	13	18	100
70	Alumina 1	11	20	20	31	35	Dead	50
	Silica	6	9	15	20	25	30	80
	Alumina 2	6	9	13	16	19	23	100
	Soil	2	4	6	8	9	13	100
	Control	2	3	4	6	8	12	100

* Ten ticks in each treatment, except controls in which only five ticks were used.
† "Almicide".
‡ "Neosyl".
§ "Alkalox 83/80".

So far as high temperatures are concerned, all adult females were found to survive 2 hr exposure to 125°F. Three hr at this temperature killed 12 per cent., and 4 hr killed 92 per cent. Two hr at 129°F killed 56 per cent. of females, and 2 hr at 138°F killed 100 per cent. Oviposition was completely prevented by 5 hr at 125°F, 3 hr at 129°F, or 1 hr at 138°F.

Relative humidity has little influence on the survival of the adult female under normal circumstances, and the loss of body water at low humidities *in vitro* is slow. However, it was found that treatment with inert dusts greatly accelerated water loss, so that in most cases death occurred before oviposition commenced. Even a sample of dry soil taken at random from the laboratory grounds, and dusted on ticks significantly

increased rate of water loss at 40 per cent. relative humidity, the lowest value tested. The trend at other relative humidities was confirmatory (Table 5). Weighings, after a certain period, actually comprise both ticks and their eggs, but information obtained by W. J. Roulston (unpublished data) suggests that the laying of the eggs does not affect gross rate of water loss.

(*b*) *Egg*

(i) *Relation of Order of Deposition to Percentage Hatch and Developmental Period of Eggs.*—The data presented in Table 6 indicate

TABLE 6

PERCENTAGE HATCH AT 95-99 PER CENT. RELATIVE HUMIDITY OF DAILY EGG OUTPUT OF B. MICROPLUS FEMALES FOR FIRST 11 DAYS OF OVIPOSITION*

Temperature (°F)	Percentage Hatch of Eggs Laid on:										
	Day 1	Day 2	Day 3	Day 4	Day 5	Day 6	Day 7	Day 8	Day 9	Day 10	Day 11
77	91.6 (435)†	93.2 (500)	92.6 (500)	92.4 (500)	95.6 (502)	95.2 (500)	92.4 (500)	77.6 (462)	82.5 (216)	80.0 (62)	79.3 (28)
80	97.0 (505)	97.4 (500)	92.4 (500)	94.8 (500)	98.4 (500)	97.4 (500)	93.2 (445)	79.2 (241)	77.8 (151)	57.0 (68)	25.0 (35)
86	96.4 (511)	96.0 (500)	96.6 (500)	93.4 (500)	91.0 (502)	86.4 (500)	85.0 (500)	83.8 (338)	62.6 (320)	46.0 (86)	44.0 (35)

* The very small numbers of eggs laid after the 11th day were discarded.

† Numbers in brackets indicate numbers of eggs in samples.

that the percentage hatch of the eggs decreases towards the end of oviposition. Uniformity and abundance of material for study of the effects

TABLE 7

RANGE OF DEVELOPMENTAL PERIODS AT 95-99 PER CENT. RELATIVE HUMIDITY OF DAILY EGG OUTPUT OF B. MICROPLUS FEMALES FOR FIRST 11 DAYS OF OVIPOSITION*

Temperature (°F)	Range of Developmental Period (days) of Eggs Laid on:										
	Day 1	Day 2	Day 3	Day 4	Day 5	Day 6	Day 7	Day 8	Day 9	Day 10	Day 11
77	28.2-29.6	27.0-29.2	26.4-28.8	26.0-28.6	25.6-28.6	26.2-29.4	26.0-29.0	26.6-29.0	26.2-29.2	25.6-29.6	26.6-29.0
80	21.8-23.2	21.0-23.4	20.0-22.0	20.0-21.8	20.4-22.0	20.0-22.0	20.2-21.6	20.0-22.2	20.4-22.4	21.2-22.8	21.6-22.6
86	19.0-21.0	18.0-20.4	17.6-19.8	17.0-18.2	15.4-19.0	17.0-19.6	16.4-19.0	16.8-18.8	16.8-18.8	16.4-19.2	17.0-18.8

* Each figure based on mean of shortest or longest developmental periods in egg batches from five ticks. The very small numbers of eggs laid after the 11th day were discarded.

of temperature and relative humidity on development may therefore be ensured by selecting eggs laid fairly early during oviposition. Fertilization

apparently occurs as the eggs are being laid, as commonly occurs with the eggs of arthropods. The period of development is not affected by the order of deposition (Table 7).

(ii) *Effect of Temperature and Relative Humidity on the Developmental Period of the Eggs.*—Eggs for study of the effects of temperature and relative humidity were collected on the fourth day after the commencement of oviposition by females maintained at 85°F because, as indicated in Figure 1 and Table 6, maximal numbers are available then and viability is high. The influence of various combinations of temperature and relative humidity on the developmental period of such eggs is illustrated in Table 8. Only minimum developmental periods were

TABLE 8

EFFECT OF TEMPERATURE AND RELATIVE HUMIDITY ON THE MINIMUM DEVELOPMENTAL PERIOD* OF BATCHES OF EGGS OF B. MICROPLUS

All figures in this table represent the day of the first emergence of a batch. The number in brackets indicates the day on which the first hatch occurred in the majority of batches under those conditions. The other figures represent the range of the minima

Temp. (°F)	Range and Mode (in brackets) of Minimum Developmental Periods in Days of Egg Batches at Relative Humidity:						
	70%	75%	80%	85%	90%	95%	Satd.
62	No hatch		No hatch		114(117)124		113(—)146†
65				68(—)—†			70(—)—†
71			44(45)45	39(41)42			38(41)44
73	37(37)37		34(35)36		36(36)37		35(36)39
77	30(31)32						
79	No hatch	23(23)27	23(24)26	23(24)29		23(25)27	23(24)26
80							21(22)22
85	No hatch		19(20)20		17(18)18		17(18)18
95	No hatch		17(17)17		16(16)17		14(15)17

* At least several thousand eggs were studied at each combination of temperature and relative humidity.

† Only one or two eggs hatched.

recorded. It is known, however, that in almost every instance peak emergence of batches incubated at temperatures over 70°F and relative humidity approaching saturation occurred during the second day after emergence commenced. Peairs (1927) advanced reasons for concluding that the average time of the first emergence of insects at different temperatures was probably a more reliable index than the mean time of emergence.

At temperatures approaching 60°F embryonic development was usually completed, but the larvae were unable to burst the chorion. In spite of this a small emergence could be secured even at 59°F if the greater part of the development were undergone at a favourable temperature. Eggs maintained for 60 days at 59°F did not undergo any detectable development, but retained their viability, and developed when transferred to suitable temperatures.

Various mathematical formulae have been used to express the relationship between temperature and speed of development of arthropod eggs. One of these, a form of the equation for the logistic curve,

$$1/y = K/(1 + e^{a-bx}),$$

was discussed by Davidson (1942, 1944). In this equation y = incubation period in days, x = temperature in °C, and a, b, and K are constants. A curve of this form was fitted to the data of Table 8 by least squares, the numerical values for the expression being

$$100/y = 6.72425/(1 + e^{6.18167-0.25496x}).$$

Good agreement exists between the theoretical and actual values of the average percentage development per day (Fig. 2). This curve is based on

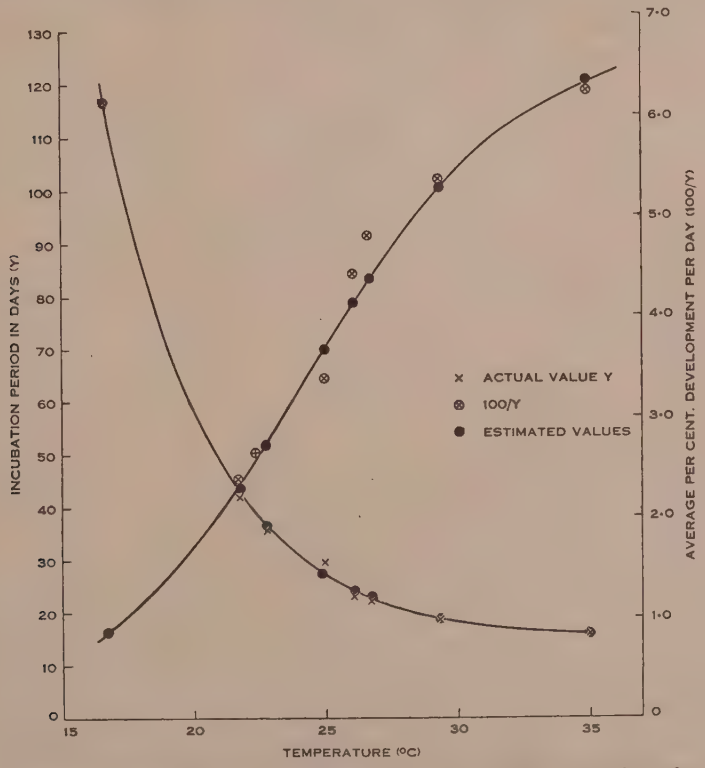


Fig. 2.—Effect of temperature on the rate of development of cattle tick eggs.

minima, and has the limitation that minima are functions of group size. The true mean developmental period of batches could not be observed accurately.

No hatching of eggs occurred at constant relative humidities lower than 70 per cent.

(iii) *Viability of Eggs at Various Constant Temperatures and Relative Humidities.*—In Table 9 are presented the results of an experiment on the influence of temperature and relative humidity on percentage hatch of the eggs of *B. microplus.* It is evident that significant hatches occur only at very high relative humidities and within the temperature range of 70-98°F.

These data indicate the need for caution in discussion of the viability of the eggs of *B. microplus.* Legg (1930), without reference to humidity conditions, quoted figures for the fertility of egg-batches varying from 68 to over 90 per cent. It is probable that the batches giving the lower emergences underwent development during periods of low relative humidity. This criticism applies with even greater force to the results quoted in an earlier Australian publication (Anon. 1917) in which fertility was stated to range from 9 to 98 per cent.

TABLE 9

PERCENTAGE HATCH* OF EGGS OF B. MICROPLUS AT VARIOUS TEMPERATURES AND RELATIVE HUMIDITIES

Temperature (°F)	Percentage Hatch at Relative Humidity:					
	70%	75%	80%	85%	95%	99%
62	0			0	5	8
65	0	0	0	1		8
70	0	0	3	3	73	95
79	0	9	26	84	95	98
85	0		50		100	100
90			90		100	100
95	0		0		100	100
98			0	1	1	50

* In most cases based on at least 300 eggs.

(iv) *Effect of Fluctuating Temperatures and Relative Humidities on Viability and Developmental Period of the Eggs.*—The influence of fluctuating temperatures on the period of development of the eggs was investigated in an incubator arranged for automatic maintenance of the temperature for 5 hr at 59°F, followed by a regular rise over 12 hr to 97°F. After 5 hr at 97°F there was a regular fall over 2 hr to 59°F. These temperatures were selected as representing approximately the extremes at which development could occur. The cycle was repeated until hatching occurred. Inside the cabinet, relative humidity fluctuated between 50 and 90 per cent. in anti-phase to the temperature. Thus, there were periods when the relative humidity was unfavourable for the eggs, but it was known that eggs placed on alternate days at 50 and 100 per cent. relative humidity gave small hatches, and therefore it was likely that some of the experimental batches would survive the daily fluctuation observed. The true mean temperature in the cabinet was 78°F. At a constant temperature

of 78°F the minimum incubation period is 25 days (Fig. 2). The eggs in this experiment commenced hatching on the 23rd day. This indicates that even with an extreme fluctuation of this type the mean temperature affords a good guide to developmental period, and that great acceleration in development as recorded by Parker (1930) in grasshopper eggs (up to 38.6 per cent.) does not occur. The possibility of a comparatively small acceleration is not to be excluded, but for all practical purposes mean temperatures could probably be used in ecological studies to determine egg development periods.

TABLE 10

EFFECT OF PERIODS AT A SUBLIMINAL TEMPERATURE* ON THE SUBSEQUENT INCUBATION PERIOD OF EGGS OF B. MICROPLUS

Temperature Before and After Period at Subliminal Temperature (°F)	Days at Subliminal Temperature	Increase in Incubation Period (days)		
		Treatment 1†	Treatment 2‡	Treatment 3§
76	1	2‖	2	2
	4	4	2	3
	8	7	8	8
	16		16	16
85	1	1	1	1
	4	3	3	3
	8	8	7	7
	16		15	15
89	1	1	1	1
	4	3	3	4
	8	10	8	8
	16		17	15
97	1	1	1	1
	4	4	4	3
	8	No hatch	8	9
	16	No hatch	No hatch	18

* 20°F.

† Eggs newly laid before exposure to 20°F.

‡ Eggs which had undergone approximately one-fourth of development before exposure to 20°F.

§ Eggs which had undergone approximately one-half of development before exposure to 20°F.

‖ Each figure based on the eggs from three ticks or a minimum of several thousand per treatment.

(v) *The Effect of Exposure to Temperatures Below the Developmental Zero on Subsequent Development of Eggs.*—To investigate whether exposure of eggs of *B. microplus* to subliminal temperatures affected the subsequent developmental period, freshly laid eggs, eggs which had completed about one-fourth, and others which had completed about one-half of their development were exposed for various periods to a temperature

of 20°F, at which, of course, no development could occur (see Fig. 2). The batches were transferred to various favourable temperatures after the period at 20°F, and the developmental period or balance of the developmental period was determined. Comparison of these figures with the expected figures at continuous constant temperature (Table 10) indicated no significant effect from the period of exposure to temperature below the developmental zero on the speed of subsequent development.

(*c*) *Larva*

(i) *Influence of Temperature and Relative Humidity on Longevity of Larvae.*—Larvae hatched from eggs maintained at 95°F were separated into batches containing from 50 to several hundred individuals. These were enclosed over humidifying solutions, and incubated at various constant temperatures. Mortality was assessed daily, larvae being considered dead if unable to walk. Observation of numerous batches indicated that once the first larval death occurred, almost all larvae in the batch died within a few days. The results of the experiment are presented in Table 11.

TABLE 11

EFFECT OF TEMPERATURE AND RELATIVE HUMIDITY ON THE LONGEVITY OF LARVAE OF B. MICROPLUS

Temperature (°F)	Maximum Longevity of Larvae in Days at Relative Humidity:								
	45%	50%	60%	65%	70%	80%	85%	90%	95%
59		13	13		90	170		200	218
72		5	7		12	40		240	190
85	3	4		6		17	25	47	80
90	3		3		4	5	5	34	27
95	1	1	2		2	4		25	29

The dependence of the larvae on high relative humidities for survival under constant conditions is evident. The maximum longevity of 240 days was recorded at 72°F and 90 per cent. relative humidity. Legg (1930) recorded a maximum of 154 days *in vitro*. It is not possible to say from the data in Table 11 whether 95 per cent. relative humidity is less favourable than 90 per cent. However, some evidence has been obtained that a saturated atmosphere is unsuitable for larvae, as they soon become lethargic, and survive for shorter periods than at slightly lower relative humidities. For example, batches of several thousand larvae derived from eggs laid at room temperature and left undisturbed where the maximum temperature did not exceed 80°F survived for 166 days at 90 per cent. relative humidity. Similar batches survived for 146 days under conditions approaching saturation.

Larvae are more vulnerable than eggs to low temperatures. For example, 16 hr at 20°F killed approximately 50 per cent., and 48 hr at 20°F killed about 90 per cent. of larvae, whereas viability of eggs remained high after 16 days at this temperature.

Some evidence has been obtained that the longevity of the larva depends to some extent on the temperature and relative humidity to which it was subjected in the egg stage. For instance, eggs laid by ticks maintained at 95 and 85°F yielded larvae which survived 47 and 90 days respectively under the same conditions of temperature and relative humidity. Further study is needed on this point, which is of great importance in relation to laboratory studies under constant conditions.

Observations also showed that longevity was influenced by activity. Cultures of larvae which were stimulated to frequent activity by disturbance lived much shorter lives than cultures left undisturbed under otherwise similar conditions.

(ii) *Water Relations of Larvae.*—Lees (1946) showed that nymphs of *Ixodes ricinus* L. were able to replenish body moisture reserves by absorption of water from the atmosphere. The ability of the larvae of

TABLE 12

LOSS OF WEIGHT BY BATCHES OF LARVAE* OF B. MICROPLUS AT 86°F AND VARIOUS RELATIVE HUMIDITIES AND SUBSEQUENT INCREASE IN WEIGHT AT 95 PER CENT. RELATIVE HUMIDITY

R.H. (%)	Period of Moisture Loss: Weight Loss at 24 hr (%)	Period of Moisture Uptake: Original Weight Regained in 24 hr (%)	Period of Moisture Uptake: Original Weight Regained in 48 hr (%)
10	25.4	14.3	25.8
20	27.1	8.8	15.9
30	21.4	5.8	8.1
40	19.3	8.6	8.7
50	13.2	7.7	9.0
60	11.0	13.2	14.0
70	7.9	5.9	7.5

* A minimum of 1500 larvae, weighing approximately 0.04 g, was used in each treatment.

B. microplus to survive long, rainless periods in the field, whereas they do not survive long at low relative humidities *in vitro* suggests that they also possess some mechanism for replenishing body fluids. Wilkinson (1953) has shown that larvae can imbibe free water from dew or other droplets. Prior to this discovery an experiment was made to investigate whether larvae can absorb moisture directly from air. Larvae which had hatched 2 weeks earlier and had been maintained thereafter at favourable temperature and relative humidity were conditioned for 24 hr at 95 per cent. relative humidity and then placed in conditioned glass tubes ventilated through cotton wool plugs in perforated rubber stoppers. Air at specified humidities was then circulated inside and outside of these tubes which were maintained at 86°F. The percentage loss of weight was determined after 24 hr. The larvae were then transferred

to 95 per cent. relative humidity at 86°F and weighed 24 and 48 hr later. The percentage moisture loss and subsequent gains are presented in Table 12.

Apparently the larvae were able to replenish body moisture losses from atmospheric moisture even in the absence of free water. In most cases, however, complete restoration of body weight lost in 24 hr had not occurred 48 hr after restoration to high relative humidity.

IV. Discussion

These studies show that each of the three non-parasitic stages of *B. microplus* has special characteristics. The engorged female adult can survive and oviposit under a wide range of temperatures and relative humidities. Oviposition may last several weeks. It can be suspended at low temperatures, and resumed on transfer of the tick to suitably high ones. The egg, on the other hand, has a relatively narrow range of temperatures and relative humidities suitable for development. High humidities and temperatures are necessary for high eclosion percentages. The duration of development of eggs varies greatly with temperature, ranging from 14 to 146 days. The response of the egg to temperature parallels that of the ovipositing adult to the extent that development can be suspended at very low temperatures and be resumed on transfer to a favourable temperature. Such periods of suspended development may be four times the minimum duration of development. The larva is the most vulnerable of the non-parasitic stages to low temperatures, but under laboratory conditions of low to moderate temperatures and high humidities it may live up to 8 months.

The bearing of the results of the laboratory studies on the practical problem of cattle tick control requires consideration. In general, the studies serve rather to draw attention to aspects of the field ecology of the tick which warrant investigation, than to provide data of direct relevance to them.

The ultimate area of distribution of the species is an important consideration, in view of the cost of quarantine measures and their interference with the free movement of cattle. *In vitro,* the non-parasitic stages, particularly the egg, require for full development conditions of high humidity, and to a lesser extent, high temperature. This dependence must be considered in relation to the behaviour of the adult female tick which, after leaving the host, migrates into and oviposits in the specialized environment of the ground level of pasture, in which humidity may be very high. Both females and eggs are able to survive periods at low temperatures, even though these inhibit development. Hence it is reasonably certain that the species could survive outside the present zone of distribution in areas where the macroclimates appear unfavourable. The determination of the suitability of a particular area must await studies of microclimatic conditions.

At present tick control measures depend principally on the application of acaricides to the host cattle, since land management techniques to combat the non-parasitic stages are difficult or impracticable. However, advantage could possibly be taken of the demonstrated vulnerability of the egg stage to low humidities, by clearing sites of dips, mustering yards, watering facilities, and other places where cattle foregather, of vegetation or debris providing moist oviposition sites for adult ticks. The practical value of this suggestion remains to be assessed.

The potentially great longevity of the unfed larvae indicates the extreme importance of the consideration of this stage in practical control measures. However, the direct application of the laboratory data on larvae to field conditions is not possible. Campbell (1952) states of *Ixodes ricinus*: "Populations maintained within enclosures to which host animals are denied access do not persist for more than a few weeks after the end of the normal season of activity. This observation is in contrast to the records of ticks enduring starvation for several years under constant controlled conditions in the laboratory." Probably a parallel statement could be made for the larvae of *B. microplus*. In the laboratory, the long-lived cattle tick larvae were kept under specialized conditions of constant temperatures and constant high relative humidities, conditions differing from those in the field. On the other hand, the association of great longevity of larvae in laboratory cultures with high humidity may have little relevance as larvae may drink water from dew drops (Wilkinson 1953). Possibly drinking is of greater significance in survival under temporary conditions of low humidity than is the ability of larvae to recoup water loss by direct absorption from the atmosphere when relative humidity is high. The relationship between the longevity of larvae and the temperatures at which the corresponding eggs were incubated also requires investigation, as does the ability of aged larvae to attach to hosts and complete their development. At Yeerongpilly, Queensland, some laboratory-raised larvae, aged 31 days, successfully parasitized host cattle to which they were applied (Snowball, unpublished data). Symons (1909) described an experiment in which larvae successfully parasitized cattle after having been maintained for 132 days since hatching in a flask at room temperature. Further data are needed on this subject.

In both control and eradication programmes, a knowledge of the length of the non-parasitic life-cycle is desirable to predict the time of appearance of successive generations. This, together with the appropriate microclimatic information, would have to be obtained in the area concerned. The summation of the various maxima of all stages, as found in these laboratory studies, to estimate the maximum non-parasitic life-cycle is to a great extent unrealistic. Apart from other considerations mentioned above, it presumes a sequence of temperatures and humidities which would only occur under artificial conditions. Hence, in an eradication programme it would not be justifiable to continue treatment of cattle,

after they become apparently free of ticks, for the maximum period of 469 days non-parasitic tick life calculated in this way (39 days pre-oviposition; last egg laid 44 days after commencement of oviposition; maximum egg developmental period 146 days; 240 days larval longevity). Nevertheless, in the absence of specific data on the field situation, this period is a guide to the time during which cattle should be kept under surveillance.

Where regulation of tick numbers is the chief concern, the minima as estimated by the laboratory studies are probably more relevant than the maxima. Perhaps the most significant feature of the laboratory results to the grazier concerned primarily with tick control is that the emergence of the progeny of a particular batch of simultaneously dropped ticks occurs over a period. Assuming that the microhabitat has temperatures averaging about 70°F, and humidities of 90 per cent. or above, the first progeny will hatch 44 days after, and the last about 77 days after the parent females drop (Tables 1, 3, 8), an emergence span of approximately 5 weeks. Therefore, single dipping treatments at widely spaced intervals cannot be expected to effect substantial reductions in larval population. The emergence span must be considered in timing dipping treatments, and in evaluating toxicants from the aspect of the length of time their residues persist on the cattle after dipping.

V. Acknowledgments

The author is indebted to Dr. H. R. Seddon, formerly Professor of Veterinary Science, University of Queensland, for laboratory accommodation during the performance of this research. Mr. G. A. McIntyre, Division of Mathematical Statistics, C.S.I.R.O., performed the statistical analyses.

VI. References

Anon. (1917).—The cattle tick in Australia. Bull. Adv. Coun. Sci. Ind. Aust. No. 1.

Arthur, D. R. (1951).—The bionomics of *Ixodes hexagonus* Leach in Britain. *Parasitology* **41**: 82-90.

Ault, C. N. (1948).—Investigaciones sobre las dificultades de combatin la garrapata *Boophilus microplus*. *Rev. Med. Vet. B. Aires* **30**: 174-211, 254-97.

Boero, J. J., and D'Angelo, E. (1947).—Biologia del *Boophilus microplus*, garrapata commun de los bovinos. Misc. Publ. Minist. Agric. B. Aires No. 236.

Campbell, J. A. (1952).—Recent work on the ecology of the pasture tick *Ixodes ricinus* L. in Britain. Rep. 14th Int. Vet. Congr., Lond. pp. 113-19.

Cooley, R. A. (1946).—The genera *Boophilus, Rhipicephalus* and *Haemaphysalis* (Ixodidae) of the New World. Nat. Inst. Hlth. Bull. No. 187.

Davidson, J. (1942).—On the speed of development of insect eggs at constant temperatures. *Aust. J. Exp. Biol. Med. Sci.* **20**: 233-9.

Davidson, J. (1944).—On the relationship between temperature and rate of development of insects at constant temperatures. *J. Anim. Ecol.* **13**: 26-38.

Gelormini, N. (1940).—Bionomia del *Boophilus microplus*. Contribucion inicial a su estudio. (N. Gelormini: Buenos Aires.) (Abstr: *Rev. Appl. Ent.* B **36**: 109 (1948).)

LEES, A. D. (1946).—The water balance in *Ixodes ricinus* L. and certain other species of ticks. *Parasitology* **37**: 1-20.

LEGG, J. (1930).—Some observations on the life history of the cattle tick (*Boophilus australis*). *Proc. Roy. Soc. Qd.* **41**: 121-32.

PARKER, J. R. (1930).—Some effects of temperature and moisture upon *Melanoplus mexicanus* Saussure and *Camnula pellucida* Scudder (Orthoptera). Bull. Mont. Agric. Exp. Sta. No. 223: pp. 1-132.

PEAIRS, L. M. (1927).—Some phases of the relation of temperature to the development of insects. Bull. W. Va. Agric. Exp. Sta. No. 208.

POUND, C. J. (1899).—Notes on the cattle tick. Its development, life history, habits, and geographical distribution. *Proc. Roy. Soc. Qd.* **14**: 28-38.

SAPRE, S. N. (1940).—The life history of *Boophilus australis* (Fuller). *Indian J. Vet. Sci.* **10**: 346-53.

SEDDON, H. R. (1951).—Diseases of domestic animals in Australia. Part 3. Tick and mite infections. Serv. Publ. Dep. Hlth. Aust. Vet. Hyg. No. 7.

SYMONS, S. T. D. (1909).—The cattle tick: tick infestation, tick fever and preventitive measures. Publ. Dep. Agric. N.S.W. Stock Branch No. 7.

WILKINSON, P. R. (1953).—Observations on the sensory physiology and behaviour of larvae of the cattle tick, *Boophilus microplus* (Can.) (Ixodidae). *Aust. J. Zool.* **1**: 345-56.

CYTOLOGICAL STUDIES ON THE SPECIFIC DISTINCTNESS OF THE OVINE AND BOVINE "STRAINS" OF THE NEMATODE *HAEMONCHUS CONTORTUS* (RUDOLPHI) COBB (NEMATODA: TRICHOSTRONGYLIDAE)

By K. C. Bremner*

(*Manuscript received March* 7, 1955)

Summary

The studies reported here follow the conclusions of Roberts, Turner, and McKevett (1954) that the ovine and bovine "strains" of *Haemonchus contortus* (Rudolphi 1803) Cobb 1898 are distinct species. The cytology of the two forms has been investigated and it was found that the chromosome number for each form was $2n = 11(\delta), 12(\varphi)$. The autosomes of each form measure 3 μ in length and, whereas the *X*-chromosomes of the worms from sheep are similar in size to the autosomes, the *X*-chromsomes of the worms from cattle attain a size of 8 μ.

Fertile hybrid females were obtained in a cross-breeding experiment and were also seen in a natural, mixed infestation. These, however, appeared in only small numbers and, furthermore, as they were never seen in animals with pure infestations as judged by the type of larva, it seemed evident that some fertility barrier is present.

Some discussion is given to the host specificity of the two forms and further evidence is brought forward to support previous conclusions that some degree of host specificity is present. It is concluded that the restricted degree of interbreeding encountered, together with considerations of host specificity, support the claims of Roberts, Turner, and McKevett (1954) that the two forms are separate species.

I. Introduction

The specific distinctness of the ovine and bovine "strains" of *Haemonchus contortus* (Rudolphi 1803) Cobb 1898 has been studied by Roberts, Turner, and McKevett (1954). These workers noted that the infective larvae could be readily separated on appearance and that this visual distinctness could be expressed by significant differences in total length, tail length, and also in the ratio of total length to tail length. Significant differences were also found in the lengths of the spicules of the males and in the distances of the hooks from the tips of the spicules. They also reported that whereas the vulval process may show a wide range of shapes and sizes, those of females from cattle were mainly short and rounded, and those of females from sheep were mainly long and linguiform. These differences were found to remain stable despite a change of host. Attention was also directed to some degree of host specificity, and in a single trial carried out to test the possibility of interbreeding it was found

* Division of Animal Health and Production, C.S.I.R.O., Veterinary Parasitology Laboratory, Yeerongpilly, Qld.

that the infective larvae remained true to type and could readily be distinguished visually. On the basis of these differences, these workers decided that two distinct species existed. The name *H. contortus* (Rudolphi 1803) Cobb 1898 was retained for the species normally occurring in sheep, and the name *H. placei* (Place 1893) Ransom 1911 was referred to the species normally occurring in cattle. It was admitted, however, by Roberts, Turner, and McKevett (1954) that these differences were not as rigid as might be expected between distinct species. Also the single experiment on which they based their evidence of the presence of a fertility barrier was carried through only to the F_1 generation.

Following the development of simple squash techniques, cytology has given promise of being a valuable aid to the taxonomist. Boyes and Wilkes (1953), for example, have prepared a key differentiating the larvae of 16 species of Tachinidae (Diptera) on chromosome morphology alone. Dobzhansky and Epling (1944) have also shown that, though indistinguishable morphologically, the flies *Drosophila pseudoobscura* Frolowa 1929 and *D. persimilis* Dobzhansky & Epling 1944 have a different chromosome structure, and by cross-breeding experiments demonstrated the existence of partial hybrid sterility between the two species. Cytology, however, has rarely been used in nematode taxonomy. Koidzumi, Hiraishi, and Koino (1925) reported that *Ascaris lumbricoides* from man displayed a haploid chromosome number differing from that of *A. lumbricoides* from pigs, but this work has not been confirmed. Only one paper (Threlkeld and Henderson 1941) has been found in the literature in which the cytology of *H. contortus* is discussed and this work was confined to the form infesting sheep.

It was therefore considered that cytological examination of the two forms of *H. contortus* might assist in determining their taxonomic status, and a preliminary report of this work has already been published (Bremner 1954).

II. Methods

Only living material was used, as this allowed greater ease of dissection and gave the most successful squash preparations. Adult worms were obtained immediately after slaughter of calves and sheep, and kept in 0.7 per cent. sodium chloride solution in an incubator at 37°C. Thirty minutes before dissection, the worms were removed in batches of six and placed in 0.5 per cent. saline with the object of creating a hydrostatic pressure within the body cavity. All dissections were carried out in this concentration under a dissection microscope and on a ground-glass slide strongly illuminated from above. By this means, the extreme tips of gonads could be located easily and a rapid, transverse cut just anterior to these resulted in about a third of the gonad being ejected from the body cavity by the sudden release of the hydrostatic pressure. The tips of the gonads were then cut off in preparation for squashing.

The squash method employed was a modification of Slizynski's (1952) technique. The gonad tips were transferred with dissecting needles to a small drop of 45 per cent. acetic acid on a dry, albuminized slide. It was found that if excess acid were used, the contained cells were expelled forcibly and became widely scattered over the slide after squashing, causing considerable waste of time when the slide was searched later for suitable metaphase plates. This was avoided by using only the minimum volume of fixative necessary to float the gonad off the point of the needle (about 2 cu. mm.) and immediately covering the gonad with a piece of "Cellophane" about 2 cm square. This in turn was covered with a similar square of blotting paper and the preparation subjected to maximum thumb pressure. The blotting paper was then removed and the slide immersed in 45 per cent. acetic acid to ensure adequate fixation. This also allowed the "Cellophane" square to float free of the squashed material. The slide was next transferred to aceto-orcein stain for 45 min. Far better staining was achieved with Gurr's synthetic orcein than with orcein prepared from natural sources. After staining, the squashes were dehydrated, cleared, and mounted in "Xam". In order to ensure accuracy of chromosome counts, at least five metaphase plates were examined in each squash.

III. Experimental Results

(*a*) *Natural Infestations*

Naturally acquired infestations in calves and sheep were examined first and the chromosome number in gonial cells was found to be the same for worms from either host, namely $2n = 11(\delta), 12(\varphi)$. Threlkeld and Henderson (1941) who used sectioned material quoted numbers of $2n = 9(\delta), 10(\varphi)$ for worms obtained from sheep, but stated that these were only tentative.

Whereas gonial metaphase spreads from both male and female worm from sheep contained chromosomes all having approximately the same length of 3 μ (Plate 1, Figs. 1 and 2), those from worms of cattle origin included two giant chromosomes in the female and one in the male with a length of about 8 μ (Plate 1, Figs. 3 and 4). These large chromosomes are undoubtedly *X*-chromosomes. Autosomes of worms from cattle had dimensions similar to those of the worms from sheep.

The positive heteropycnosis exhibited by these large chromosomes along their complete length during prophase of gonial mitosis (Plate 1, Fig. 5) indicated that they were composed mainly of heterochromatin. *X*-chromosomes of worms from sheep could be distinguished from the autosomes by their squat shape at metaphase, but exhibited positive heteropycnosis only along a small region at one end during gonial prophase. The detection of heterochromatin in resting nuclei by its appearance as chromocentres was not possible and nucleoli were never seen. Sachs (1953) reported a similar behaviour of the heterochromatin in the short-tailed field mouse *Microtus agrestis* Linnaeus 1761 in which

chromocentres are formed in resting spermatogonia, but not in nuclei of cells of other tissues. Sachs suggested that this behaviour was probably due to the different metabolic activities of the cells concerned, since Darlington and La Cour (1940) had shown that the reaction of heterochromatin can be physiologically conditioned. However, Caspersson (1947) has pointed out that an exact definition of heterochromatin seems to be very difficult, and White (1954) has suggested that "what we ordinarily refer to as euchromatin and heterochromatin are merely the two ends of a continuous series of different types of 'chromatins'." This latter hypothesis seems to offer the most satisfactory explanation for the atypical behaviour of the heterochromatin of *H. contortus*.

Few preparations showed the positions of centromeres or constrictions, and where visible, these could rarely be seen in more than one chromosome in any gonial metaphase plate. Consequently autosomes could not be distinguished from one another in either strain. Whenever a constriction was seen in any chromosome it was invariably metacentric in position, and never more than one constriction was seen in any chromosome. Clear preparations of meiotic divisions could not be obtained from squashes of either testes or ovaries. Accurate localization of the positions of centromeres was therefore not possible.

TABLE 1

DISTRIBUTION OF CYTOLOGICAL TYPES IN FEMALE H. CONTORTUS FROM NATURAL INFESTATIONS

Host	No. of Hosts Examined	No. of Worms Examined	No. of Worms with Giant *X*-Chromosomes	No. of Worms with Small *X*-Chromosomes
Calf	5	96	96	0
Sheep	7	135	6	129
Goat	2	67	0	67

In all, 50 male and 298 female *H. contortus* from natural infestations were examined. Twenty-five males were collected from sheep and an equal number from calves. The giant *X*-chromosome was displayed by all the males of cattle origin, and was not seen in any of the males of sheep origin. Results of the observations on female worms are shown in Table 1. One female obtained from a goat possessed a triploid make-up of 18 equal-sized chromosomes (Plate 1, Fig. 6). This triploid individual displayed a morphology similar to that of the diploid form, with the exception of the gonial cells, which were obviously much larger than corresponding diploid cells. In view of the increased volume of nuclear material present this was only to be expected. However, the infrequent occurrence of this aberrant form indicated that it was of no taxonomic importance.

It will be observed that all females from cattle displayed giant *X*-chromosomes, whereas of the females from sheep, only 4.4 per cent. of

a total of 135 examined showed this type of *X*-chromosome. The females from the goats were evidently of sheep origin as they all possessed small *X*-chromosomes.

(*b*) *Experimental, Pure Infestations*

Since one of the sheep examined was found to be carrying a few worms with a chromosome morphology typical of the form infesting calves, studies were extended to pure, artificial infestations.

A worm-free calf was infested with larvae obtained from cattle and was slaughtered when the worms had reached maturity. Thirty-five females were examined and all displayed metaphase plates containing two giant chromosomes. Of these females, 29 possessed small, rounded, vulval processes, two had large linguiform processes, and four had processes of one or other of the other types referred to by Roberts, Turner, and McKevett (1954) as "intermediate". Thus these results confirmed those obtained from natural infestations in cattle, and also showed that the six females from sheep set down in Table 1 as possessing giant chromosomes must have originated from cattle-type larvae. It is also apparent that there is no direct relationship between the presence of large *X*-chromosomes and the type of vulval flap.

An attempt to infest a second calf with sheep-type larvae proved unsuccessful, this presumably being a manifestation of the host specificity referred to by Roberts, Turner, and McKevett (1954).

(*c*) *Experimental, Mixed Infestations*

Having demonstrated the existence of a cytological dimorphism related to the differences in adult and larval morphology cited by Roberts, Turner, and McKevett (1954), the question of interbreeding was next considered, and it may be seen that hybridization would give rise to a cytologically distinguishable female possessing one large and one small *X*-chromosome. Since similarity of the autosomes of each form made it impossible to distinguish hybrid males, examinations for evidence of hybridization were confined to female worms. It may be noted at this stage that no hybrids were found among the 298 females obtained from natural infestations.

In an experiment designed to determine if hybridization would occur when the two forms were brought together in the one host, a worm-free lamb was given a mixture of 7000 larvae from sheep and 7000 larvae from cattle, the sheep being selected as the host in order to avoid possible interference by host resistance mechanisms. A second worm-free lamb was then dosed with 10,000 larvae obtained from the first lamb. This culture constituted a sample of the F_1 generation at the larval stage and was composed of 28 per cent. cattle-type and 72 per cent. sheep-type larvae.

The lamb carrying the worms of the parent generation was then slaughtered and the female worms were examined morphologically and cytologically. About 2000 worms were scraped off the walls of the

abomasum and placed in a one-litre cylinder of water, the cylinder then being agitated until the worms were well dispersed. About 100 ml of liquid was poured off immediately, and the females present in the sample were sorted into three groups on the basis of the type of vulval process each possessed. Of the 93 females obtained, 51 per cent. had small rounded processes (cattle-type), 42 per cent. had large linguiform processes (sheep-type), and 7 per cent. displayed other types (Roberts, Turner, and McKevett 1954).

The lack of agreement between the distribution of larval types among the offspring and the distribution of types of vulval processes among the parents cannot be explained. It may be that some host specificity prevented the females of cattle origin from producing eggs as prolifically as the females of sheep origin, but no experimental evidence is known that would support this supposition.

TABLE 2

HYBRIDIZATION IN MIXED INFESTATIONS OF SHEEP AND CATTLE H. CONTORTUS

Distribution of karyotypes among selected P generation females

Karyotype	Type of Vulval Process	No. of Worms
12 Small chromosomes	Large and linguiform	39
	Small and rounded	4
	Intermediate	4
10 Small + 2 large	Small and rounded	42
11 Small + 1 large (hybrid)	Small and rounded	1
18 Small chromosomes (triploid)	Large and linguiform	1

Cytological examination was not made at random. Instead, an attempt was made to examine equal numbers of each dominant morphological type, but this was prevented by mortalities among the worms retained for dissection. The results of these observations are shown in Table 2, where it will be noted that among the 91 worms dissected, one female was found displaying the expected hybrid karyotype (Plate 1, Fig. 7). It is interesting to note that one female displayed a triploid make-up, and was the second female of this type to be seen in these studies.

Six weeks after infestation the lamb carrying the F_1 generation was showing a faecal egg count of 12,000 e.p.g.* with a differential larval count of 13 per cent. cattle-type larvae and 87 per cent. sheep-type larvae. The lamb was then slaughtered and 77 female *H. contortus* were selected from it, approximately equal numbers of each of the two dominant morphological types being collected. Of these females, 50 displayed the sheep-form karyotype, 24 showed the cattle-form karyotype, and three disclosed the hybrid make-up.

* e.p.g. = eggs per g of faeces.

Eggs were taken from the uterus of each of these 77 worms and cultured in separate vessels of tap water at room temperature. Later examination disclosed that active first stage larvae had hatched from all but two of the egg samples and these two were from females with sheep-type chromosome complements. Thus this experiment was important in that it demonstrated the fertility of hybrid females as well as the viability of eggs obtained from such females.

The distribution of the two dominant types of vulval processes in the random sample taken of the P generation indicates that worms of both ovine and bovine origin were present in approximately equal numbers. If mating were at random, 50 per cent. of the F_1 generation would be expected to have a hybrid karyotype. If the differential counts on larvae obtained from the P generation are considered to be a more reliable criterion of its constitution, it could be assumed that adults of the two strains were present in a 1 : 5 ratio. In this case a proportion of 27.7 per cent. hybrids would be expected in the F_1 generation on the basis of a Hardy-Weinberg equilibrium, namely,

$$p^2 : 2p(1 - p) : (1 - p)^2,$$

where p = the frequency of the giant *X*-chromosome. However, the number of hybrids detected in this cross-breeding experiment approximated only 4 per cent. of the females examined.

(*d*) *Natural, Mixed Infestations*

The finding of fertile hybrids in the experimental, mixed infestation suggested that an examination of natural, mixed infestations would be of value. Such mixed infestations do not occur very frequently. Gordon (personal communication) states that only occasionally are cattle-type larvae seen in cultures from sheep faeces, and Roberts (personal communication), who has been studying the epidemiology of parasitic gastro-enteritis of both beef and dairy cattle for nearly eight years, has noted only one herd in which mixed infestations of the two forms regularly occur. Since a number of goats infested with sheep-type *H. contortus* graze the same pasture as the calves in this herd, it is almost certain that these goats play a major part in the maintenance of the mixed infestations. A calf from this herd was selected for slaughter when its faecal egg count for *Haemonchus* was 8200 e.p.g. and larval differentiation showed 86 per cent. cattle-type and 14 per cent. sheep-type. Of 100 female worms selected at random, 84 possessed two giant *X*-chromosomes, nine had small *X*-chromosomes, and seven were hybrids.

IV. Discussion

When attempting to decide the specific distinctness of samples drawn from two different populations, three sets of information must be considered, namely, differences in morphology and physiology, geographical relationships, and the presence or absence of reproductive isolation.

With regard to the ovine and bovine forms of *H. contortus*, differences in morphological characters and in host specificity have been referred to earlier. Further information on host specificity is provided by Porter (1953) who found that calves grazing pastures contaminated by cattle acquired appreciably more *H. contortus* than did lambs grazing the same pasture. Porter also found that in similar trials with pastures contaminated by sheep, lambs acquired more stomach worms than did calves.

Further observations by Roberts and Bremner (1955) on the calves mentioned earlier as carrying mixed infestations through an association with goats have shown that when mixed natural infestations occur in calves, maximum egg counts of the ovine form are much smaller than those of the bovine form, and that host resistance to the former is manifested

TABLE 3

FAECAL EGG COUNTS OF GOATS GRAZING CALF PASTURES

Sample Source	Total Strongyle Egg Count (e.p.g.)*	*H. contortus* Larvae (%)	
		Sheep-type	Cattle-type
Fully grown buck	165	0.6	—
Fully grown doe	Insufficient for egg count	1	—
Mixed sample from two goats 9-12 months of age	1000	31	—
Mixed sample from two goats 9-12 months of age	800	42	—
Mixed sample from two goats 2-3 months of age	1575	13	—
Mixed sample from two goats 2-3 months of age	660	43.5	1.5
Mixed sample from two goats 2-3 months of age	915	41	—

* e.p.g. = eggs per g of faeces.

at a much earlier age than to the latter. Furthermore, the resistance reactions to the two forms are quite independent of one another, and that against the sheep form is complete, resulting eventually in total elimination of this form. Faecal cultures were prepared by the author from 12 goats running with these calves, and it was interesting to find that whereas most samples contained appreciable numbers of sheep-type *H. contortus* larvae, only one culture contained cattle-type larvae, which were present only in negligible proportions. Results of these examinations are shown in Table 3. Since the goats were grazing pastures heavily contaminated with cattle-type larvae, it would appear that at the time of examination, all but one or two of these animals were strongly resistant to infestation with the bovine form, irrespective of their age.

However, of these differences between the two forms, that in karyology is the one most satisfactory for taxonomic discrimination since it allows of no overlap and, moreover, it can be used to detect hybridization.

It is difficult to assess the geographical relationship of the two forms because their distribution is entirely dependent on the distribution of their hosts and this is due solely to the activities of man. Grazing practice in Queensland tends to keep the two major hosts separate, and very few sheep are found in cattle-raising areas, while cattle grazed in sheep-breeding areas are vastly outnumbered by the sheep and are frequently run on separate pastures. Conditions pertinent to the distribution of the two forms in Queensland appear to be as follows:

(i) When grazing cattle are not in contact with sheep or goats, any infestations of *H. contortus* which exist are monomorphic for cattle-type larvae and for the cattle-form karyotype.

(ii) When grazing sheep have not been in contact with cattle, existing infestations of *H. contortus* will be monomorphic for sheep-type larvae and also for sheep-type chromosome complements.

(iii) When cattle and sheep or goats graze the same pasture, mixed infestations of the two types occur, particularly in sheep, with the production of hybrids in apparently limited numbers.

(iv) If cattle carrying mixed infestations are isolated from sheep or goats, it would be expected that the host specificity of the sheep form would ultimately result in the disappearance of this form from such cattle. That this does occur is shown by the fact that in areas in which only cattle are run only cattle-type larvae are seen in faecal cultures.

The position in respect of sheep with mixed infestations when isolated from cattle is not so clear. However, it is known that cattle-type larvae are rarely seen in cultures from sheep in sheep country and then only in small numbers. Yet it is also known that artificial infestations of the cattle form may be readily set up in sheep and maintained in this host for a number of years (Roberts, Turner, and McKevett 1954). Furthermore, outbreaks due to the cattle form have been reported in sheep under natural conditions (Roberts, Turner, and McKevett 1954). As the animals used by the author for artificial infestation were reared worm-free, and as the sheep in which natural outbreaks were reported came to the coast from areas in which the ovine form was practically non-existant (Roberts, personal communication), it may well be that sheep are protected against infestation with the cattle form through exposure to the ovine form. On the other hand, the freedom of sheep from the cattle form in the sheep areas may simply be an indication that climatic conditions in Queensland sheep country are unfavourable to it. Should either of these theories be correct, it indicates a further difference between the two forms which may be physiological or ecological in nature. In other words, it would appear that mixed infestations continue to occur

only when cattle and sheep or goats are maintained on the same pasture, or have been maintained there in the immediate past.

It seems extremely unlikely that the numerous differences exhibited by these two forms could have developed without geographical isolation occurring between two populations of an ancestral species, and White (1954) has pointed out that once they have arisen, heterochromatic regions of chromosomes can increase or decrease in the course of evolution by duplication or deletion. It would appear then that the known facts are best interpreted by assuming that at some time in the past two groups of an ancestral species of *H. contortus* became geographically isolated due to the isolation of their hosts, and began to diverge. During this period of isolation and divergence the two forms acquired a degree of host specificity and possibly some degree of reproductive isolation. Conditions may then have been altered by the breakdown of the geographical isolation, probably due to man's activities, until the present interesting set of circumstances came into existence.

The question now arises as to which of two possible taxonomic categories these forms can be assigned, that is, whether they are sub-species or separate species. If the two forms had acquired their partial host specificities without developing any degree of reproductive isolation, then meeting of populations of the two forms as a result of human interference would result in random mating with free production of hybrids. If this is so, the ovine and bovine forms of *H. contortus* should be considered separate sub-species (Mayr 1942; Mayr, Linsley, and Usinger 1953). If, however, in addition to acquiring their partial habitat preferences, the two forms had also developed partial reproductive isolation, meeting of populations of the two forms would result in the production of a number of hybrids, limited by the strength and nature of the reproductive isolating mechanism. If hybridization is relatively restricted, the two forms should be accorded separate specific status (Mayr, Linsley, and Usinger 1953) and the hybridization may be considered an "introgressive hybridization" (Anderson and Hubricht 1938) in which genes of one species are filtering into the gene pool of another. Anderson (1949) has pointed out that introgressive hybridization is observed most frequently in habitats modified by man, and Mayr, Linsley, and Usinger (1953) believe that it must be "fairly complete" to restore gradients in gene frequencies between diverging populations.

Partial host specificity has been demonstrated, but there is some doubt about the degree of reproductive isolation. It has been shown by the author that hybrid females can produce viable offspring, but it is highly significant that only three hybrids were found among the 77 F_1 females examined from the cross-breeding experiment. Also, among the females comprising the mixed, natural population infesting the calf at "Dayboro", frequencies of 76.5 per cent. cattle-type, 21.9 per cent. hybrid, and 1.6 per cent. sheep-type would be expected on the basis of a Hardy-Weinberg equili-

brium. The observed distribution of these types, however, was 84 per cent., 7 per cent., and 9 per cent. respectively. A statistical comparison of these figures shows that, where the frequency of the giant *X*-chromosome is 87.5 per cent., the probability of the two strains mating at random to produce the observed hybrid frequency of 7 per cent. is approximately 2×10^{-9}. Thus the difference between the observed and expected values is highly significant, and leaves little doubt of the existence of genetically determined agencies restricting the interbreeding of populations of the two forms.

In addition to hybrids with visibly heterozygous *X*-chromosomes, the existence should be considered of hybrids indistinguishable with the technique used. Thus it was not possible to distinguish hybrid males, and if these occurred and were not sterile, fertilization by them of females having homozygous *X*-chromosomes of a size similar to that of the male could possibly result in the occurrence of females homozygous with regard to their *X*-chromosomes, but heterozygous for one or more autosomes. Whether such hybrids do occur and are fertile remains a matter of speculation.

The basic issue is, of course, the amount of gene exchange between populations of the two forms which are in contact, and Patterson and Stone (1952) sum up the modern species concept by stating that "in sexual forms, a species consists of the members of a population or group of populations which can exchange genes freely with each other, but which can cross to members of no other form (or population) sufficiently to lose their separate genetic identity."

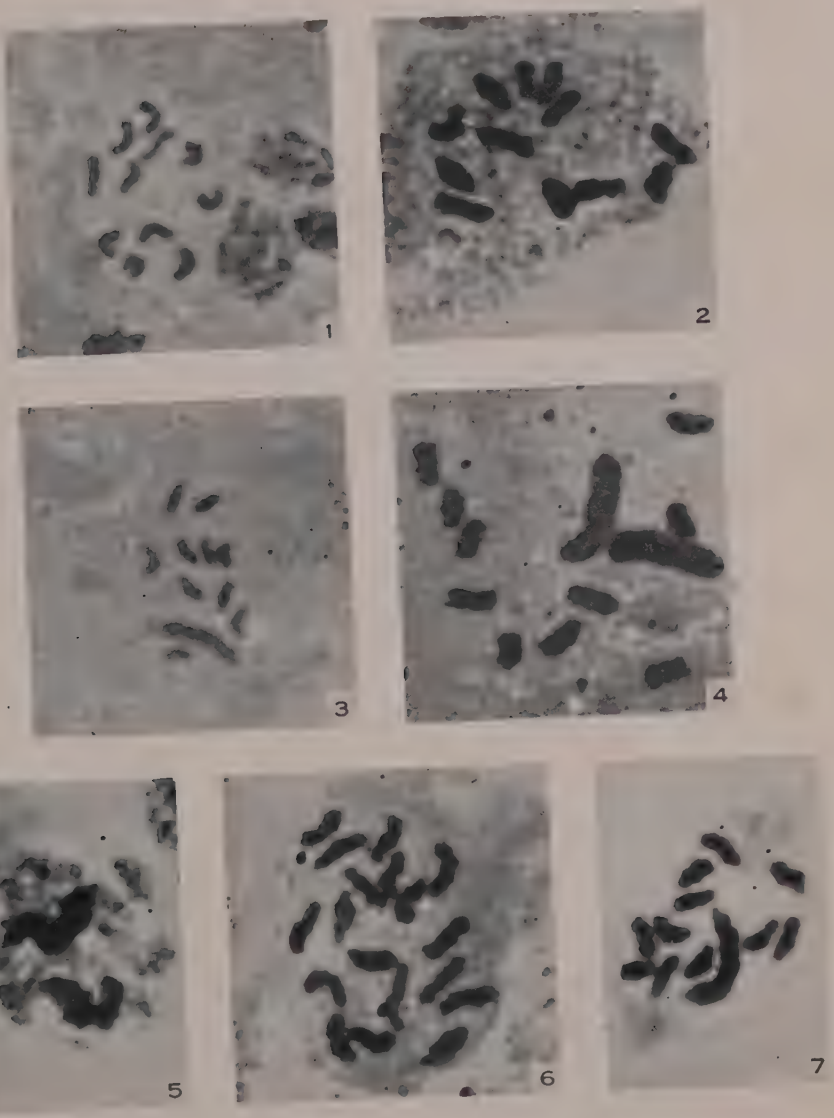
In the final analysis it must be poined out that over the centuries, populations of both forms of *H. contortus* must have come into contact innumerable times so that interbreeding was possible, yet both forms have maintained their characteristic differences in morphology and karyology. In other words, they appear to have retained their separate genetic identity. It is concluded, then, that the results of this cytological study strongly favour the elevation of the ovine and bovine strains to separate specific status.

The above findings refer to the strains of *H. contortus* occurring in sheep, goats, and cattle in Queensland. It is highly probable that the form occurring in cattle elsewhere is similar to that discussed in this paper. Worms identified as *H. contortus* have also been recorded from a number of wild ruminants, and it may be interesting to see whether these forms are comparable cytologically to those found by the author in sheep and cattle, or whether further karyotypes exist.

V. Acknowledgments

The author wishes to express his thanks for the continued interest and guidance of Dr. F. H. S. Roberts, Veterinary Parasitology Laboratory, Yeerongpilly, and for the advice of Mr. W. B. Mather, Department of

CYTOLOGY OF HAEMONCHUS CONTORTUS



Zoology, University of Queensland, especially with regard to techniques. Thanks are also due to Mr. R. K. Keith, C.S.I.R.O., for the photography and larval differentiations.

VI. References

Anderson, E. (1949).—"Introgressive Hybridization." (John Wiley & Sons Inc.: New York.)

Anderson, E., and Hubricht, L. (1938).—*Amer. J. Bot.* **25**: 396.

Boyes, J. W., and Wilkes, A. (1953).—*Canad. J. Zool.* **31**: 125.

Bremner, K. C. (1954).—*Nature* **174**: 704.

Caspersson, T. (1947).—"Nucleic Acid." In Soc. Exptl. Biol. Symposium No. 1. (Cambridge Univ. Press.)

Darlington, C. D., and La Cour, L. (1940).—*J. Genet.* **40**: 185.

Dobzhansky, T. H., and Epling, C. (1944).—Publ. Carneg. Instn. No. 544.

Koidzumi, M., Hiraishi, S., and Koino, H. (1925).—Far-East. Ass. Trop. Med. Rep. No. 6 p. 335.

Mayr, E. (1942).—"Systematics and the Origin of Species." (Columbia Univ. Press: New York.)

Mayr, E., Linsley, E. G., and Usinger, R. L. (1953).—"Methods and Principles of Systematic Zoology." (McGraw Hill: London.)

Patterson, J. T., and Stone, W. D. (1952).—"Evolution in the Genus *Drosophila*." (Macmillan: New York.)

Porter, D. A. (1953).—*Amer. J. Vet. Res.* **14**: 550.

Roberts, F. H. S., and Bremner, K. C. (1955).—*Aust. Vet. J.* **31**: 133.

Roberts, F. H. S., Turner, H. N., and McKevett, M. (1954).—*Aust. J. Zool.* **2**: 275.

Sachs, L. (1953).—*Heredity* **7**: 228.

Slizynski, M. B. (1952).—*Drosophila Inform. Serv.* **26**: 134.

Threlkeld, W. L., and Henderson, M. E. (1941).—*Virginia J. Sci.* **2**: 172.

White, M. J. D. (1954).—"Animal Cytology and Evolution." 2nd Ed. (Cambridge Univ. Press.)

Explanation of Plate 1

Fig. 1.—Spermatogonial metaphase chromosomes of *H. contortus* from a sheep. × 2000.

Fig. 2.—Oogonial metaphase chromosomes of *H. contortus* from a sheep. × 3000.

Fig. 3.—Spermatogonial metaphase chromosomes of *H. contortus* from a calf. × 2000.

Fig. 4.—Oogonial metaphase chromosomes of *H. contortus* from a calf. × 3000.

Fig. 5.—Prophase oogonium of *H. contortus* from a calf showing positive heteropycnosis of the giant *X*-chromosomes. × 3000.

Fig. 6.—Oogonial metaphase chromosomes of a triploid *H. contortus* from a goat. × 3000.

Fig. 7.—Oogonial metaphase chromosomes of the hybrid form of *H. contortus*. × 3000.

MORPHOLOGICAL STUDIES ON THE MICROFILARIAE OF *ONCHOCERCA GIBSONI* CLELAND & JOHNSTON AND *ONCHOCERCA GUTTUROSA* NEUMANN (NEMATODA: FILAROIDEA)

By K. C. Bremner*

(*Manuscript received February* 17, 1955)

Summary

Studies have been made on the morphology of the microfilariae of *Onchocerca gibsoni* Cleland & Johnston, and *O. gutturosa* Neumann. Examinations were initially made on larvae emerging from dissected female worms, and later, on larvae recovered from the skin. No differences in either morphology or body length measurements were detected between the skin-inhabiting and freshly emerged larvae of each species. The form, size, and arrangment of the caudal and cephalic nuclei were found to vary widely within each species. Of the many measurements investigated only that of body length had any taxonomic value. Skin-inhabiting microfilariae of *O. gibsoni* had a body length of 240-280 μ (mean 266 μ), whereas those of *O. gutturosa* measured only 200-260 μ (mean 224.5 μ), the difference between the means being highly significant.

I. Introduction

At one time *Onchocerca gibsoni* Cleland & Johnston 1910, which forms "worm nodules" in cattle, was a cause of serious economic loss to the cattle industry in Australia. Numerous attempts to ascertain its life-history during this period were unsuccessful (Gilruth and Sweet 1911; Heydon 1927). Nowadays, the losses due to its presence are of little significance (Seddon 1950), but it still seemed desirable that its life-history should be known.

Observations commenced in Brisbane some years ago by Roberts (personal communication) demonstrated that a large proportion of cattle infested with *O. gibsoni* were also infested with *O. gutturosa* Neumann 1910. *O. lienalis*† Stiles 1910 was also found in some animals, but its incidence did not appear to be as high as that of the other species. As the microfilariae of at least two of these species, namely *O. gibsoni* (Heydon 1927) and *O. gutturosa* (Steward 1937), occur in the skin, it became apparent that life-history studies on *O. gibsoni* could not be commenced unless some character was available whereby the microfilariae of these two species could be distinguished. Animals infested with *O. gibsoni* alone could then be selected for study, or possibly, when the two species were

* Division of Animal Health and Production, C.S.I.R.O., Veterinary Parasitology Laboratory, Yeerongpilly, Qld.

† According to Steward (1937), *O. lienalis* and *O. gutturosa* are probably synonymous.

present, differences could be detected in the distribution of their microfilariae in the skin.

Measurements have proved of great assistance in distinguishing the microfilariae of some species of Filariidae, but a search of the literature revealed that measurements recorded for *O. gutturosa* and *O. gibsoni* showed some disagreement (Gilruth and Sweet 1911; Steward 1937; Buckley 1938; Gibson 1952). As these differences could have been due to different or possibly unsuitable techniques of preparation, it was felt that a comparison of measurements should be attempted on specimens prepared by a standardized method. Gibson's (1952) work on the identification of the microfilariae of *O. volvulus* (Leuckart 1893) of man, *O. reticulata* (Diesing 1841) of the horse, and *O. gutturosa* of cattle indicated that the form, size, and arrangement of the caudal and cephalic nuclei were of value in distinguishing these three species, and accordingly these nuclei were also studied. Gibson's findings appeared particularly promising in view of Sandground's (1934) failure to find any morphological difference between *O. volvulus* and *O. gibsoni*.

II. Methods

Studies were made initially on microfilariae freshly emerged from females dissected from cattle within 15 min of slaughter, and placed in ox serum for about 5 hr at room temperature. Adults of *O. gibsoni* were obtained as nodules from the brisket area and those of *O. gutturosa* from the connective tissue of the ligamentum nuchae and scapular cartilage. Care was taken to avoid damage to the adult worms with possible liberation of immature larvae. The microfilariae were concentrated by centrifugation and prepared for examination as thick smears. The smears were air-dried, fixed in methyl alcohol for 5 min, and stained in a 1 in 20 dilution of Giemsa stain for 30 min.

Skin samples were taken with a skin punch shortly after the slaughter of cattle and prepared for examination by slicing into thin ribbons less than 1 mm in width, which were placed in ox serum. To ensure a reasonably pure culture of microfilariae of *O. gutturosa*, skin samples were confined to cattle without any obvious infestation with *O. gibsoni* and were restricted to the area of the withers. Skin samples considered most likely to yield only microfilariae of *O. gibsoni* were taken from the brisket region.

Measurements on microfilariae in stained, thick smears were made with the assistance of a camera lucida. Some measurements on body length were also made on microfilariae liberated from the female worms and from skin into physiological saline and killed by gentle heat. Larvae killed by this technique lay straight and could be measured quickly. As will be shown later in this paper, the body length of larvae killed by heat showed little if any difference from that of larvae prepared by fixation and staining.

III. Results

(*a*) *Cephalic and Caudal Nuclei*

To avoid possible variation due to positional differences, drawings of the cephalic and caudal nuclei of both species were confined to larvae

Fig. 1.—Variations in arrangement of cephalic and caudal nuclei of microfilariae *O. gibsoni* and *O. gutturosa.*

which lay with their excretory pore directed to the right-hand side of the field.

Gibson (1952), from his observations in Guatemala on the microfilariae of *O. gutturosa* obtained from skin samples, described the cephalic nuclei as consisting of "two large anterior tandem nuclei followed by a single large nucleus in the midline of the larva" and the caudal nuclei as composed of "a long terminal bar . . . preceded by large quadrangular nuclei which are more or less confluent." In the author's studies, no differences in the nuclei as regards size, form, arrangement, or reaction to staining could be detected between freshly-born and skin-inhabiting larvae of either species. In both species the arrangement of the cephalic nuclei was found to vary widely. Only approximately 5 per cent. of *O. gutturosa* larvae displayed the single median third nucleus described by Gibson (1952) and although a tandem pair of anterior nuclei was observed in most cases, many larvae had a single anterior nucleus or a row of three abreast. Similarly, no one typical arrangement of cephalic nuclei was seen among the microfilariae of *O. gibsoni,* and larvae of the two species

TABLE 1

BODY LENGTH MEASUREMENTS OF FRESHLY-BORN MICROFILARIAE OF O. GIBSONI AND O. GUTTUROSA

Species	Heat-Killed			Fixed and Stained		
	No. of Larvae	Range (μ)	Mean and S.D. (μ)	No. of Larvae	Range (μ)	Mean and S.D. (μ)
O. gibsoni	140	240-320	263.6 ± 10.8	81	242-286	265.4 ± 8.6
O. gutturosa	125	200-260	229.2 ± 9.8	80	197-259	228.0 ± 13.8

could not be differentiated on these characters. Caudal nuclei of most larvae of *O. gutturosa* conformed to the arrangement and form described by Gibson, but this applied equally well to some larvae of *O. gibsoni.* Some of the variations in the arrangement and form of these nuclei in the two species as seen by the author are shown in Figure 1.

(*b*) *Measurements*

Body length measurements of microfilariae of both species obtained from freshly dissected females are compared in Table 1, where both heat-killed and fixed and stained larvae are considered. The data show firstly that the two methods of preparation for body length measurement used by the author gave approximately the same results, and also that the difference between the means for each species is highly significant (standard error of difference for heat-killed larvae = 1.26, and for fixed and stained larvae = 1.8).

Microfilariae obtained from the skin samples collected by the method already outlined were next measured after killing by heat. Those from the brisket area measured 240-280 μ (mean 266 μ, S.D. 6.0) and those from the withers 200-260 μ (mean 224.5 μ, S.D. 11.5). Frequency distributions of these larvae are given in Figure 2. These ranges and means fall within

the measurements of freshly-born *O. gibsoni* and *O. gutturosa* larvae respectively, to which species it is considered they can be assigned with a reasonable degree of accuracy. If this assumption is correct, it seems therefore that the larvae of these two species do not alter in body length between the time of emergence from the female and when they appear in the skin.

Measurements were also made from stained preparations of the relative distances of certain larval structures from the anterior end of the larva. These are set down in Table 2, which shows that none of them could be used as criteria for taxonomic discrimination.

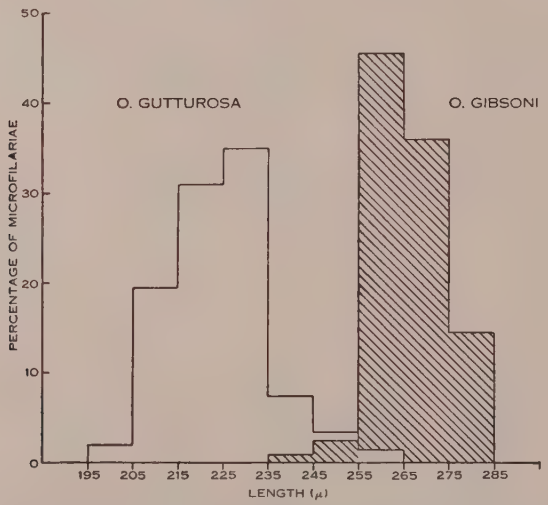


Fig. 2.—Frequency distribution of body lengths of microfilariae of *O. gibsoni* and *O. gutturosa* recovered from skin samples.

IV. Discussion

Gibson's (1952) conclusion that the microfilariae of *O. volvulus*, *O. reticulata*, and *O. gutturosa* could be readily distinguished by the form, size, and arrangement of the caudal and cephalic nuclei did not apply to the microfilariae of *O. gibsoni* and *O. gutturosa*. Indeed, the arrangement of cephalic nuclei in microfilariae of *O. gutturosa* examined by the author showed a wide range of variation. Arrangements of cephalic nuclei similar to that figured and discussed by Gibson as typical of this species were seen, but did not appear to be of any more frequent occurrence than any of the other types illustrated in Figure 1.

In contrast to the observations of Kershaw (1948) on the development of the microfilariae of *Litomosoides carinii* (Travassos 1919) Chandler 1931, newly-emerged larvae of both *O. gibsoni* and *O. gutturosa* displayed

a detailed morphology identical with that of the forms occurring in the skin. It would appear therefore that the larvae of *Onchocerca* spp. are mature when born and undergo little, if any, change between birth and ingestion by their respective intermediate hosts.

Of the many measurements made only that of body length was of any value as a distinguishing character. There is some overlapping in the lengths of the two species, namely among larvae of *O. gutturosa* with maximum measurements and larvae of *O. gibsoni* with minimum measurements, but the degree of overlap is so slight that this measurement enables approximately 90 per cent. of the larvae to be assigned to their correct species. It is interesting to note that body length of these microfilariae

TABLE 2

MEASUREMENTS OF SIGNIFICANT STRUCTURES IN MICROFILARIAE OF O. GIBSONI AND O. GUTTUROSA

Structure	Measurement from Anterior End Expressed as Percentage of Body Length			
	O. gibsoni		*O. gutturosa*	
	Range	Mean and S.D.	Range	Mean and S.D.
First nucleus	1.7-3.2	2.5 ± 0.4	2.0-3.5	2.8 ± 0.5
Ant. margin nerve ring	14.2-28.4	22.5 ± 2.9	17.0-28.2	24.9 ± 2.2
Post. margin nerve ring	16.4-29.7	24.8 ± 2.9	19.4-29.9	26.9 ± 2.1
Excretory pore	25.4-37.8	32.7 ± 2.9	34.1-40.6	36.8 ± 1.8
Anal pore	79.1-85.9	83.5 ± 1.6	83.3-91.1	86.0 ± 2.7
End of nuclear column	96.7-98.6	97.7 ± 0.5	94.8-98.6	96.9 ± 0.8

did not undergo any change between birth and their appearance in the skin as has been recorded for other species of Filaroidea (Kershaw 1948). Kershaw (loc. cit.) also drew attention to considerable differences in body length between microfilariae of *L. carinii* lying along the periphery and those in the centre of thick films which he considered to be caused by different rates of drying in the film. However, no such differences were noted in the measurements made from thick films by the author, and it may be that larvae of *Onchocerca* spp. respond less rapidly to osmotic changes than do those of *L. carinii*.

Very few measurements of either *O. gibsoni* or *O. gutturosa* are available in the literature. For *O. gibsoni*, the body length of freshly-born microfilariae is quoted by Gilruth and Sweet (1911) as from 230-350 μ, and by Buckley (1938) as from 230-270 μ. The larvae measured by these workers had emerged from nodules and their measurements show a smaller minimum length than those obtained by the author from the same source, namely 240-320 μ. The only body length measurements recorded for *O.*

gutturosa are by Steward (1937) and Gibson (1952), namely 150-220 μ and 189-251 μ (227 $\mu \pm 16.1$) respectively. In both cases the larvae measured came from the skin. The author's measurements for skin-inhabiting larvae of this species are 200-260 μ (mean 224.5 μ), which compare favourably with the measurements recorded by Gibson. Steward's measurements are smaller but this may have been due to the fact that he examined only a few larvae and did not fix them while fresh.

V. Acknowledgment

The writer is indebted to Dr. F. H. S. Roberts, Veterinary Parasitology Laboratory, Yeerongpilly, for his advice and interest.

VI. References

Buckley, J. J. C. (1938).—*J. Helminth.* **16**: 121.

Gibson, C. L. (1952).—*Amer. J. Trop. Med. Hyg.* **1**: 250.

Gilruth, J. A., and Sweet, G. (1911).—"*Onchocerca gibsoni*: The Cause of Worm Nodules in Australian Cattle." p. 24. (Dep. Trade and Customs Aust.)

Heydon, C. M. (1927).—*Aust. J. Exp. Biol. Med. Sci.* **4**: 61.

Kershaw, W. E. (1948).—*Ann. Trop. Med. Parasit.* **42**: 377.

Sandground, J. H. (1934).—"Onchocerciasis with Special Reference to the Central American Form of the Disease." Part 2, p. 155. (Harvard Univ. Press: Cambridge, Mass.)

Seddon, H. R. (1950).—Diseases of domestic animals in Australia. Part 1. Serv. Publ. Dep. Hlth. Aust. Vet. Hyg. No. 5.

Steward, J. S. (1937).—*Parasitology* **29**: 212.

A NEW SENSE ORGAN IN THE HEAD OF THE MOSQUITO AND OTHER NEMATOCEROUS FLIES

By M. F. Day*

(*Manuscript received May* 6, 1955)

Summary

A previously undescribed paired sense organ has been found in the heads of adult mosquitoes and other Nematocera. The unusual structure of this sense organ prompts the suggestion that it might be concerned with the detection of changes in pressure.

I. Introduction

A pair of sense organs previously undescribed has been observed in the head of adult *Aedes aegypti* (L.). Subsequently these organs were found in members of the following families of Diptera Nematocera: Rhyphidae, Cecidomyidae, Sciaridae, Mycetophilidae, Psychodidae, Culicidae, Chironomidae, Tipulidae.

These sense organs have not been located after careful search in sections of the head of the stratiomyid *Neoexaireta spinigera* Wied. or in the head of *Musca domestica* L., but the difficulties of locating such a structure are increased in the Brachycera by the presence of the ptilinum. However, no such organ has been reported in many thorough studies of the anatomy of the Brachycera.

II. Methods

Fixation was by alcoholic Bouin's fluid. Most of the sections were cut at 10 μ and were stained by Mallory's triple stain. Sections stained by Bodian's protargol method were useful for some details.

III. Description of the Sense Organ

The organ, for which the name tambour organ would seem to be appropriate, exhibits surprising uniformity in structure in most members of the eight families listed above. It is bilaterally symmetrical and is located between and just above the antennae (Fig. 1). The organ consists typically of the following components (Fig. 2):

(1) The cuticle forms a shallow depression between the antennae in all forms studied except the Tipulidae. In the mosquito, as in most Nematocera, this depression is so inconspicuous as to be practically invisible upon external examination. In the Tipulidae the organ is readily visible on external examination of the head (Fig. 3) and I am greatly indebted to Professor C. P. Alexander for checking this in

* Division of Entomology, C.S.I.R.O., Canberra, A.C.T.

many genera. He finds that in four genera (*Longurio*, *Megistocera*, *Hexatoma*, and *Rhabdomastix*) in which the males have enlarged frontal tubercles and greatly elongated antennae the organ is very conspicuous. It is less marked in the females of these genera, and in both sexes of some groups (e.g. *Nephrotoma* and *Dolichopeza*) external signs of the organ are almost absent.

The cuticle is of the same thickness as that of the remainder of the head. On the surface it is covered in most genera examined by many minute spines.

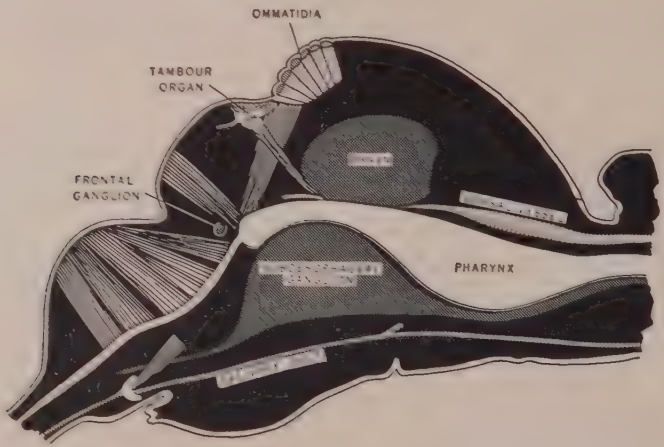


Fig. 1.—Longitudinal section of the head of female *A. aegypti* showing the location of the tambour organ.

(2) The hypodermis is considerably hypertrophied in mosquitoes, but is frequently reduced in the other insects studied. In the mosquito a circular group of hypodermal cells, about eight cells across, are enlarged to form a minute body having the shape of an inverted dome.

(3) The tracheal bulb. Immediately beneath the hypodermis is a cavity, either barrel-shaped as in the mosquito and Tipulidae or flattened, as in the other species studied. The thin walls of this cavity have circular thickenings like taenidia; a trachea runs anteriorly from the structure and it appears that the structure is, in fact, the enlarged end of a trachea.

(4) The receptor cells are arranged beneath the tracheal bulb in the form of a flattened ovoid body. The cells are dorso-ventrally flattened and radiate from the centre of this body. The receptor cells are enclosed within a sheath continuous with that of the nerve innervating the organ. A peculiar feature of the receptor cells is that two or three cells are frequently seen projecting into the tracheal bulb. No con-

nection has been found between the receptor cells and the enlarged hypodermal cells.

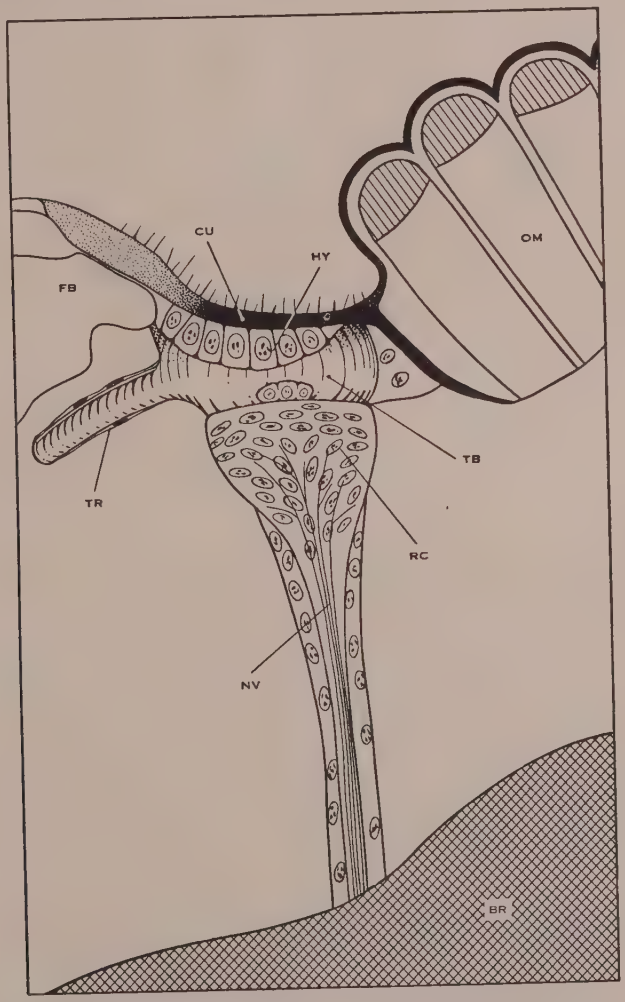


Fig. 2.—Longitudinal section of the tambour organ of *A. aegypti* showing its structure. *CU*, cuticle; *FB*, fat body; *HY*, epidermal cells; *NV*, nerve; *OM*, ommatidia; *RC*, receptor cells; *TB*, tracheal bulb; *TR*, trachea.

(5) The nerve innervating the organ runs to the brain, either directly (female *A. aegypti* and most other species examined) or after joining that from the organ on the other side (male *A. aegypti*). The nerves are robust and the nerve trunk is invested by an unusually complex cellular sheath.

It will be apparent that the most unusual feature of the sense organ is its relationship to the tracheal system. No other example of a tracheal bulb like that described above has been observed elsewhere in these insects.

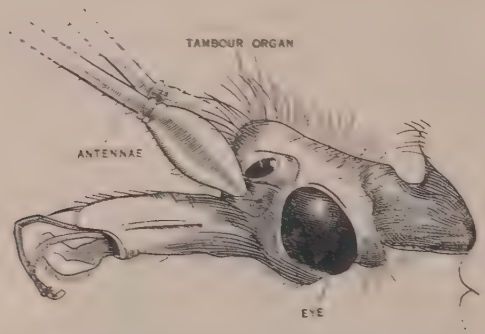


Fig. 3.—Head of the tipulid *Longurio*, showing the external appearance of the highly developed tambour organ.

IV. Discussion

Nuttall and Shipley (1903) describe on the head of the adult mosquito minute spines that probably correspond in position to those found covering the cuticle of the sense organ. However, neither they, nor other authors who studied the mosquito head (e.g. Kulagin 1905, or Thompson 1905) described the sense organ. The absence of reports of the organ is probably explained by its small size, its inconspicuous external appearance, and the occurrence of the precerebral dilator muscles of the pharyngeal pump and the retractor muscle of the cibarial pump (see Snodgrass 1944) which often confuse the appearance of the organ in histological preparations.

In the mosquito the organ has a superficial similarity in appearance to an ocellus. When the organ was found in several families of Nematocera in which ocelli are absent it was thought that it may have arisen as a modified ocellus. However, the finding of the organ well developed in several families with conspicuous ocelli indicated that this suggestion was false. There is no reason to suspect that the organ is absent from any Nematocera, or that it is present in Brachycera. The organ may be homologous with Eltringham's organ that is found in certain families of Lepidoptera (see Ehnbom (1948) for a discussion of the homologies of this structure).

The peculiar structure of the organ gives some basis for suggestions of its function. It would not appear to be adapted as a hygroreceptor or thermoreceptor and in any event these functions have been ascribed to the antennae (Roth 1951; Willis and Roth 1952). The histological structure

is vastly different from that of the radiant heat receptors located in a similar position in the grasshopper (Slifer 1951). Similarly, the auditory function has been assigned to Johnston's organ in the antennae (Roth 1948). It is not likely to be a carbon dioxide receptor, as it is present in both bloodsucking and non-bloodsucking species. The position of the organ suggests that it probably reacts to external stimuli reaching the head. The occurrence of the tracheal connection to the tracheal bulb suggests that the organ may react to pressure changes, perhaps during flight, like the air speed indicator described by Hollick (1940) on the antennae of *Muscina*. Weis-Fogh (1950) described an organ having this function in the grasshopper, but the structure of this also is very different from that of the organ found in the Nematocera.

V. Acknowledgments

Several colleagues collected and identified the insects used in this work. Thanks are due particularly to Mr. I. F. B. Common, Mr. A. L. Dyce, and Dr. S. J. Paramonov. Dr. R. E. Snodgrass, U.S. National Museum, kindly confirmed that the organ has not previously been described, and Dr. C. P. Alexander, University of Massachusetts, examined many Tipulidae to determine the occurrence of the organ in this family. The illustrations are the work of Mr. L. A. Marshall.

VI. References

Ehnbom, K. (1948).—Studies on the central and sympathetic nervous system and some sense organs in the head of neuropteroid insects. *Opusc. Ent. Suppl.* 8: 1-162.

Hollick, F. S. J. (1940).—The flight of the dipterous fly, *Muscina stabulans* Fallen. *Phil. Trans.* 230: 357-90.

Kulagin, N. (1905).—Der Kopfbau bei *Culex* und *Anopheles*. *Z. wiss. Zool.* 83: 285-335.

Nuttall, G. H. F., and Shipley, A. E. (1903).—Studies in relation to malaria. II. The structure and biology of *Anopheles*. *J. Hyg., Camb.* 3: 166-215.

Roth, L. M. (1948).—A study of mosquito behaviour. *Amer. Midl. Nat.* 40: 265-352.

Roth, L. M. (1951).—Loci of sensory end-organs used by mosquitoes (*Aedes aegypti* (L.) and *Anopheles quadrimaculatus* (Say) in receiving host stimuli. *Ann. Ent. Soc. Amer.* 44: 59-74.

Slifer, E. H. (1951).—Some unusual structures in *Locusta migratoria migratorioides* and their probable function as thermoreceptors. *Proc. Roy. Soc.* B 138: 414-37.

Snodgrass, R. E. (1944).—The feeding apparatus of biting and sucking insects affecting man and animals. *Smithson. Misc. Coll.* 104: 1-113.

Thompson, M. T. (1905).—Alimentary canal of the mosquito. *Proc. Bost. Soc. Nat. Hist.* 32: 145-202.

Weis-Fogh, T. (1950).—An aerodynamic organ in locusts. Proc. 8th Int. Congr. Ent. Stockholm. pp. 584-8.

Willis, E. R. and Roth, L. M. (1952).—Reactions of *Aedes aegypti* (L.) to carbon dioxide. *J. Exp. Zool.* 121: 149-79.

COPROPHAGY IN THE EUROPEAN RABBIT (*ORYCTOLAGUS CUNICULUS*) IN AUSTRALIA

By K. Myers*

(*Manuscript received March* 16, 1955)

Summary

Coprophagy is a normal feature in the biology of the wild rabbit (*Oryctolagus cuniculus*) in Australia.

The evidence presented shows that coprophagy occurs normally during the daily period of inactivity when rabbits are below ground. When feeding activities commence in the afternoon on the surface, coprophagy ceases. Evidence suggests that the passage of normal pellets continues throughout the night, the formation and ingestion of soft pellets recommencing when the rabbit population as a whole again moves below ground into the warrens, in the early hours of daylight.

Kittens commence ingesting soft pellets as soon as they leave the nests to feed on green grass, although suckling continues for some time.

There appears to exist a seasonal influence on the normal daily rhythm in eating of faeces. In winter less time is spent in ingesting soft pellets and more in green-feeding than in autumn and spring. It is suggested that coprophagy assumes its greatest importance to the animal during summer when rabbits are below ground for a greater proportion of the day than at any other season. During summer, also, green feed is scarce and the standing pastures are dry. It is evidently during this season that rabbits are forced to obtain from their food all the nutriment possible.

Observations show that the switchover from the production of one type of pellet to the other may be either immediate or delayed.

I. Introduction

Since Madsen (1939) brought to light an early publication of Morot's (1882) which first recorded the habit of coprophagy in the rabbit, a great deal of interest in that phenomenon has been aroused. It is now common knowledge that the rabbit passes two kinds of faeces—one an ordinary, hard, fibrous pellet passed by domesticated rabbits during the day, the other a softer and smaller type passed during the night. The soft pellets are eaten direct from the anus, without mastication, and can be recovered from the cardiac portion of the stomach (Plate 1, Fig. 1).

Madsen (1939), Taylor (1940), and Eden (1940*a*, 1940*b*, 1941) all confirmed Morot's observations and attempted to obtain some physiological explanation for the event. It was generally concluded that soft pellets are formed of material derived from the caecum, where prolonged fermentation by bacteria releases protein enclosed by fibrous material that is normally voided and lost in hard pellets. This protein is considerably enriched by bacterial protein which would also be lost.

* Wildlife Survey Section Field Station, C.S.I.R.O., Albury, N.S.W.

Coprophagy also appears to be a vital factor in vitamin economy. From the results of an experimental study on the excretion of B vitamins, Kulwich, Struglia, and Pearson (1953) calculated that coprophagy provides the rabbit with about 83 per cent. more niacin, 100 per cent. more riboflavin, 165 per cent. more pantothenic acid, and 42 per cent. more vitamin B_{12} than would be available if the soft faeces were not consumed.

Taylor (1940) suggested that the daily rhythm in laboratory rabbits might be reversed in wild rabbits, but it was left to Southern (1942) to demonstrate that this was so. He not only showed that refection was a common habit of the wild animals but also that it took place in a rhythmic manner, with the main period occurring in daylight hours and a shorter one in the middle hours of the night. Although Southern (1942) pointed out the existence of this rhythm, his interpretation was based essentially

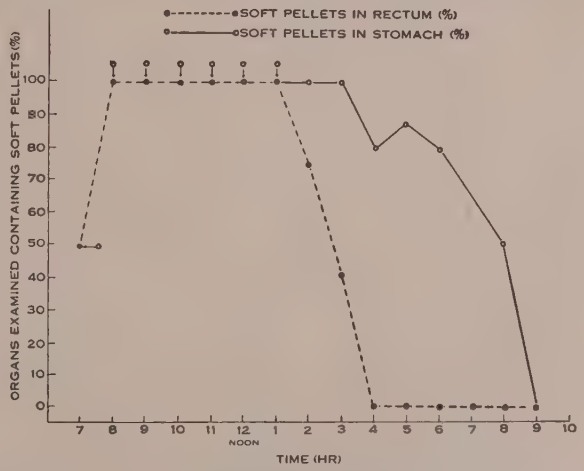


Fig. 1.—Coprophagy in the rabbit in autumn, Gunbower, April-May 1950.

upon examination of stomach contents. Owing to the lag period between the time of ingestion of pellets and the time when the pellets become unrecognizable as digestion proceeds, stomach examination alone does not give an accurate picture of the daily occurrence of refection.

The observations described in this paper add to those of Southern (1940, 1942). They were carried out as occasion permitted during field studies with myxomatosis over the past three years. The data were obtained from two localities in the Riverina region and bordering the Murray River, which divides the States of New South Wales and Victoria. Gunbower is situated on the Victorian side of the river about 190 miles west of the foothills of the Great Dividing Range. Rutherglen is situated 30 miles west of the foothill zone, also on the Victorian side of the river.

The average annual rainfall decreases steadily from Rutherglen in the east (22 in.) to Gunbower in the west (17 in.).

Data collected on breeding, both with respect to seasonal occurrence and litter size, and on body weights, show no marked locality differences. Gunbower lies within an extensive irrigation system which nullifies to some extent differences in pastures concomitant with lower rainfall. For these reasons it is believed that all the observations made can be regarded as reasonably comparable.

II. Daily and Seasonal Rhythms in Refection in the Wild Rabbit

(*a*) *Methods*

In all the rabbits examined the following criteria were noted (i) the presence or absence of soft or hard pellets in the rectum (Plate 1, Figs. 2 and 3), (ii) the presence or absence of undisintegrated pellets in the

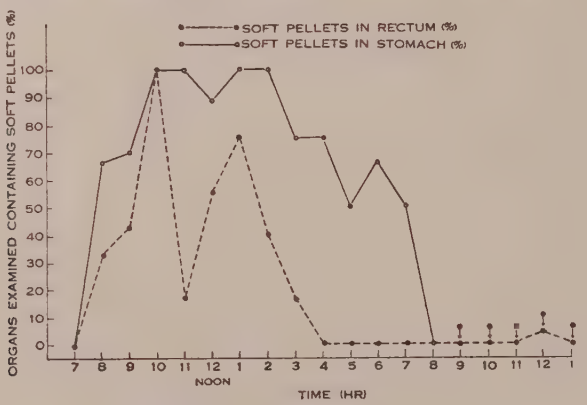


Fig. 2.—Coprophagy in the rabbit in winter, Gunbower, June-July 1950.

stomach (Plate 1, Fig. 1), (iii) rectum containing soft pellets following or followed by hard pellets, and (iv) rectum empty (Plate 1, Fig. 4).

Rabbits were collected throughout most days and dissected immediately upon capture. In order to gain the hourly time-table of the rhythm in refection, rabbits had to be obtained while underground within their warrens. These were mostly dug out, but on one occasion large numbers were collected when flooded out during irrigation procedures at Gunbower. In all cases the time of capture was noted.

(*b*) *Observations*

The observations made are presented in Tables 1-4 and are graphed as percentages in Figures 1-4. The nature of the daily rhythm is demonstrated. There seems to be little doubt that the only attribute which could be added by more efficient sampling would be a smoothing of the graphs.

(i) *The Daily Time-table.*—In the daily rhythm in refection of the rabbits from the populations sampled there are two distinct periods of switchover from the passage of one type of faeces to the other, one during the afternoon, the other during the early hours of daylight. While underground throughout the day, soft pellets are passed and refected. During the night, when above-ground feeding occurs, normal hard pellets are voided.

Observations on feeding behaviour of the populations concerned were also made at the same time as sampling took place. At Gunbower in April 1950, although the rabbits were emerging from their warrens between

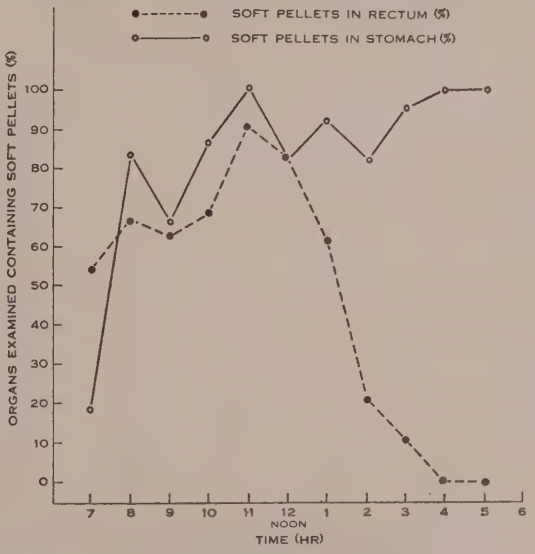


Fig. 3.—Coprophagy in the rabbit in spring, Rutherglen, September-October 1950.

3 and 4 p.m., refection began to diminish while the rabbits were still underground at 1 p.m. (Fig. 1). By the time rabbits commenced to leave the warrens a large proportion were already passing hard pellets. From stomach examinations, however, soft pellets remained recognizable until 8 p.m.—4-5 hr after refection had ceased (Fig. 1). During 2 months' observations on this population of rabbits, numbering some thousands, refection on the surface was observed twice only.

In the mornings it was also noticed at this time that rabbits were going underground at approximately 8 a.m. Here again, it is apparent that the switchover from normal to soft pellet production commenced before the period of above-ground activity ceased. No actual cases of switchover were observed during this period, but it seems altogether likely that this was merely due to the incomplete nature of sampling.

(ii) *Seasonal Differences.*—The samples taken covered the autumn, winter, and spring. It is obvious that during the winter and spring refection started later in the morning and ceased earlier in the afternoon than in autumn. Accompanying this, the rabbits were surfacing earlier in the afternoon, between 2 and 3 p.m., and remaining above ground longer in the morning, basking in the weak sun.

There are no values to hand to show what happens during the hotter months of summer. In December 1950, however, during concentrated observations on a rabbit population at Rutherglen, soft pellets were observed on the surface of the ground for the first time. These were presumed to be the final clearing of the rectum preparatory to passing

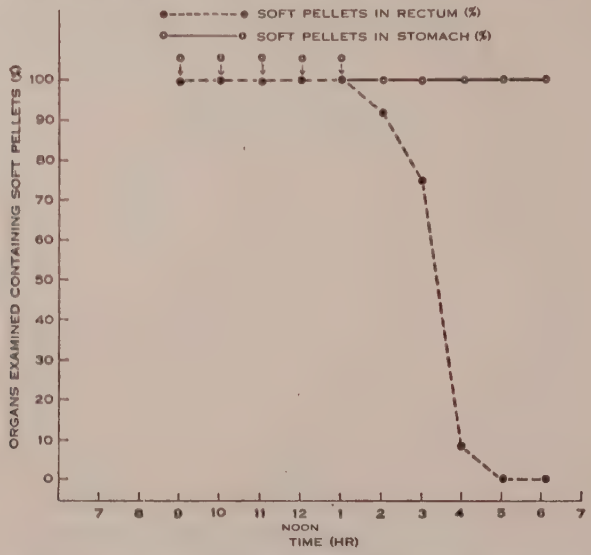


Fig. 4.—Coprophagy in the rabbit in autumn, Rutherglen, April-May 1951.

hard pellets. On several days in succession separate deposits of this kind, numbering up to 15 per day, were noticed. At this period rabbits were coming above ground at 5 p.m. and entering the warrens before 7 a.m. It seemed very likely, therefore, that refection was occurring much later in the day than had been observed during autumn, winter, and spring. It was also probable, in view of the earlier observations, that refection was commencing earlier than during the other periods.

In winter at Gunbower (Fig. 2) while it was possible to find soft pellets in the stomachs of most rabbits collected throughout the day, the evidence from rectal observations suggested a much more disturbed rhythm than that occurring in the warmer autumn (Fig. 1). Examination of the stomachs showed that the rabbits were also taking green feed at

odd intervals of the day. During these intervals refection ceased and normal hard pellets were voided.

In spring (Fig. 3) the Rutherglen sample showed a partial return to the more perfect daily cycle of autumn. It was again noticeable that although collections at set times throughout the day showed many rabbits not refecting, stomach examinations revealed that the majority had at some time during the day passed and ingested soft pellets.

TABLE 1

REFECTION IN THE WILD RABBIT IN AUTUMN: GUNBOWER, APRIL-MAY 1950

Time of Day	Rectum				Stomach		Rabbits Dissected*
	Soft Pellets	Hard Pellets	Soft Followed by Hard Pellets	Empty	Soft Pellets	No Soft Pellets	
0700	2	1	0	1	2	2	4
0800	1	0	0	0	1	0	1
0900	11	0	0	0	11	0	11
1000	17	0	0	0	17	0	17
1100	3	0	0	0	3	0	3
1200	5	0	0	0	5	0	5
1300	3	0	0	0	3	0	3
1400	14	9	1	0	24	0	24
1500	6	9	1	1	17	0	17
1600	0	5	0	0	4	1	5
1700	0	25	0	0	22	3	25
1800	0	5	0	0	4	1	5
1900	0	1	0	0	1	0	1
2000	0	2	0	0	1	1	2
2100	0	3	0	0	0	3	3

* Total number examined = 126.

The autumn sample from Rutherglen (Fig. 4) is presented to compare with Figure 1 from Gunbower. As far as it goes, it can be seen that it agrees completely with the autumn data from Gunbower both in the shape of the curve and the time of switchover.

(iii) *Age at Commencement.*—The tabulated observations all refer to weaned rabbits. During the course of dissections, 76 suckling kittens were examined, ranging in weight (paunched) from 2 oz to 1 lb 7 oz (50-650 g). Of these, 39 were either nestlings or had just left the nest, falling within a 2-5 oz (50-150 g) weight group. Examination of their stomachs showed the presence of milk alone.

The youngest rabbits found refecting were a litter of three, weighing 6 oz (170 g) and refection was found to occur widely throughout the group weighing 6 oz to 1 lb 7 oz (170-650 g). Stomach examinations of these kittens almost invariably showed a mixture of milk, green grass, and

pellets in varying proportions. Obviously, refection commences at a very early age.

(iv) *Differences in Individual Rabbits.*—In Tables 1-4, values are included for observations on rabbits in the process of changing over from soft to hard pellet production. In some rabbits, soft pellet formation had ceased completely and the rectum had emptied. Where this occurred it was usual to see the last soft pellets at the anal end of the rectum although completely empty recta were frequently found. In many rabbits hard pellets could be seen under formation in the colon while the rectum was

TABLE 2

REFECTION IN THE WILD RABBIT IN WINTER: GUNBOWER, JUNE-JULY 1950

Time of Day	Rectum				Stomach		Rabbits Dissected*
	Soft Pellets	Hard Pellets	Soft Followed by Hard Pellets	Empty	Soft Pellets	No Soft Pellets	
0100	0	22	0	0	0	22	22
0700	0	1	0	0	0	1	1
0800	1	2	0	0	2	1	3
0900	3	4	0	0	5	2	7
1000	8	0	0	0	8	0	8
1100	1	5	0	0	6	0	6
1200	10	8	0	0	16	2	18
1300	3	1	0	0	4	0	4
1400	1	3	1	0	5	0	5
1500	1	9	1	1	9	3	12
1600	0	20	0	0	15	5	20
1700	0	2	0	0	1	1	2
1800	0	3	0	0	2	1	3
1900	0	2	0	0	1	1	2
2000	0	2	0	0	0	2	2
2100	0	19	0	0	0	19	19
2200	0	23	0	0	0	23	23
2359	1	22	0	1	1	23	24

* Total number examined = 182.

either empty or emptying. In contrast with this, many cases were noted where hard pellet formation followed immediately upon cessation of soft pellet formation. In Plate 1, Figure 4, this is shown to be the case for a rabbit taken during the afternoon switchover period. Here, the two types of pellet were not only touching, but one pellet in the junction zone was both soft and fibrous.

III. DISCUSSION

The observations recorded here raise two questions of considerable interest, viz. the nature of the mechanism controlling the switchover from the production of one type of pellet to the other, and the value of refection

to the animal in nature. The fact that the switchover anticipates, by more than one hour, the change in the rabbits' activity with which the rhythm of refection is correlated, suggests that a rather complicated mechanism might be involved.

The observations made suggest that coprophagy is of greater importance to the rabbits in the areas studied during autumn and probably summer, than in winter and spring, since more hours are spent in refecting during the hotter, drier months than during the colder and wetter months. Falling, as it does, within a zone of predominantly winter rainfall, the region from which rabbit samples were collected shows great contrasts between the dry pastures of summer and autumn and the wet, green

TABLE 3

REFECTION IN THE WILD RABBIT IN SPRING: RUTHERGLEN, SEPTEMBER-OCTOBER 1950

Time of Day	Rectum				Stomach		Rabbits Dissected*
	Soft Pellets	Hard Pellets	Soft Followed by Hard Pellets	Empty	Soft Pellets	No Soft Pellets	
0700	6	3	0	2	2	9	11
0800	4	1	0	0	5	1	6†
0900	5	3	0	0	6	2	8
1000	15	5	0	2	19	3	22
1100	10	1	0	0	11	0	11
1200	5	1	0	0	5	1	6
1300	8	4	0	1	12	1	13
1400	1	23	5	0	24	5	29
1500	1	17	1	0	18	1	19
1600	0	21	0	0	21	0	21
1700	0	5	0	0	5	0	5

* Total number examined = 151.

† In one rabbit taken at 0800, the rectum contained hard followed by soft pellets.

pastures of winter and spring. The main period of breeding also occurs during winter and spring when plenty of green feed is available.

It appears altogether likely, therefore, that refection bears importantly on rabbit nutrition, assuming more importance in the life of the animal when the available nutrient, including vitamin content of pastures, falls and fibre content rises, and when the most valuable food is concentrated in seeds and roots. Nevertheless, it still occurs during winter and spring on a large scale and must add to the nutrition of rabbits even with the presence of a copious supply of green food.

If this is true, the findings of the physiologists, especially Eden (1940*b*), and Kulwich, Struglia, and Pearson (1953) give some sense of meaning to the field picture. As summer and autumn are the periods of

food scarcity, refection could allow the rabbits of the region to utilize the available food more efficiently.

The observations on kittens suggesting that refection commences in the life of a rabbit as soon as it starts to feed on grass, irrespective of the fact that it is still suckling, would make it appear that the process is, in fact, vital for the digestion of green food.

In the wild rabbit in Australia, exposed to seasonal exigencies of an extreme nature, refection may have become one of the features of its biology which allows it to colonize marginal zones where its numbers are

TABLE 4
REFECTION IN THE WILD RABBIT IN AUTUMN: RUTHERGLEN, APRIL-MAY 1952

Time of Day	Rectum				Stomach		Rabbits Dissected*
	Soft Pellets	Hard Pellets	Soft Followed by Hard Pellets	Empty	Soft Pellets	No Soft Pellets	
0900	8	0	0	0	8	0	8
1000	6	0	0	0	6	0	6
1100	10	0	0	0	10	0	10
1200	2	0	0	0	2	0	2
1300	22	2	0	0	24	0	24
1400	12	4	6	2	24	0	24
1500	0	22	2	0	24	0	24
1600	0	14	0	0	14	0	14
1800	0	4	0	0	4	0	4

* Total number examined = 116.

limited by harsh environmental conditions, both with respect to utilization of available food and water economy. In any case, it seems likely that it may be important in allowing the rabbit to populate successfully the hundreds of thousands of square miles of country where droughts of shorter or longer duration are common events.

IV. ACKNOWLEDGMENTS

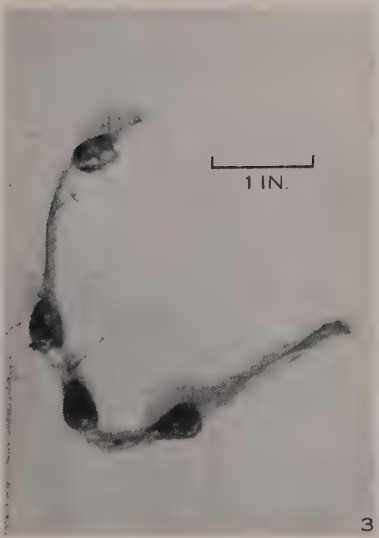
Mr. F. N. Ratcliffe, Mr. B. V. Fennessy, and Mr. J. Calaby, Wildlife Survey Section, C.S.I.R.O., are gratefully thanked for helping with dissections and for critical discussions during the preparation of the paper. Mr. C. R. G. Reid, Gunbower, Victoria, is also thanked for allowing part of the work to be carried out on his property, and Mr. L. A. Marshall, Division of Entomology, C.S.I.R.O., for preparing the figures.

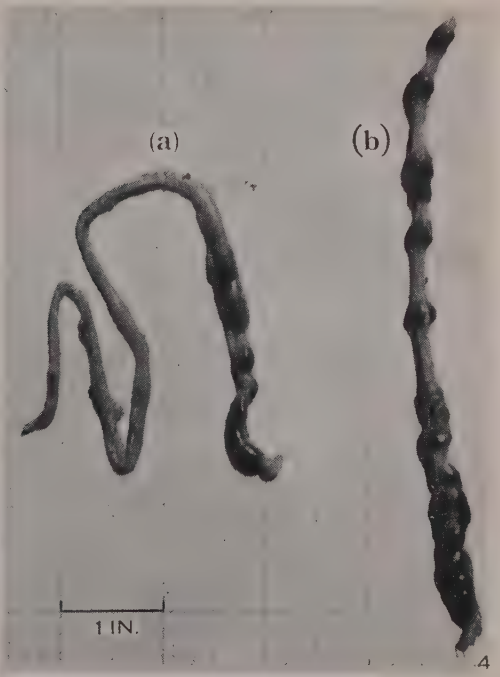
V. REFERENCES

EDEN, A. (1940*a*).—Coprophagy in the rabbit. *Nature* 145: 36-7.

EDEN, A. (1940*b*).—Coprophagy in the rabbit: origin of night faeces. *Nature* 145: 628-9.

COPROPHAGY IN THE AUSTRALIAN RABBIT





EDEN, A. (1941).—Studies on the excretion of copper in the rabbit. *J. Agric. Sci.* **31**: 145-60.

HARDER, W. (1949).—On the morphology and physiology of the caecum of rodents. *Zool. Anz. Supp.* **14**: 95-109.

KULWICH, R., STRUGLIA, L., and PEARSON, P. B. (1953).—The effect of coprophagy on the excretion of B vitamins by the rabbit. *J. Nutrit.* **49**: 639-45.

MADSEN, H. (1939).—Does the rabbit chew the cud? *Nature* **143**: 981.

MOROT, CH. (1882).—Des pelotes stomacales des leporides. *Mém. Soc. Centr. Méd. Vét.* 12 Sér. 1. Paris (quoted by Madsen (1939)).

SOUTHERN, H. N. (1940).—Coprophagy in the wild rabbit. *Nature* **145**: 262.

SOUTHERN, H. N. (1942).—Periodicity of refection in the wild rabbit. *Nature* **149**: 553-4.

TAYLOR, E. L. (1940).—The demonstration of a peculiar kind of coprophagy normally practised by the rabbit. *Vet. Rec.* **52**: 257-62.

ADDENDUM

Harder (1949), in a review of coprophagy in rodents, mentions that rabbits living on green food develop normally when completely deprived of soft pellets ("caecotrophe"). When on dry food, however, a definite loss in body weight occurs if rabbits are not allowed to eat soft pellets or if they ingest soft pellets that have been heated to 105°C. Important effective components of soft pellets therefore appear to be present in green food. This is supported by our observations suggesting a higher incidence of coprophagy in rabbits in the hot, dry summer months than at other times of the year.

EXPLANATION OF PLATE 1

Fig. 1.—Stomach opened to show disposition of faecal pellets in cardiac region. The pyloris is filled with digesting greens ingested the previous night. The stomach is from a rabbit captured at midday in autumn.

Fig. 2.—External appearance of rectum crammed full with soft pellets. Note the angular form due to mutual pressure.

Fig. 3.—External appearance of rectum containing hard pellets.

Fig. 4.—External appearance of rectum during switchover from evacuation of soft to hard pellets. (*a*) Last few soft pellets followed by empty rectum. (*b*) Soft pellets followed immediately by hard pellets.

THE RELATIONSHIP BETWEEN LARVAL AND ADULT SIZE OF THE AUSTRALIAN SHEEP BLOWFLY *LUCILIA CUPRINA* (WIED.)

By L. G. Webber*

(*Manuscript received May* 23, 1955)

Summary

Quantitative formulations are derived for the relationships between the adequacy of larval food, the weight of puparia, the length of thorax of adult flies, the number of ovarioles in adults, and the size and weight of eggs produced by adults of *Lucilia cuprina* (Wied.). Smaller adults grown from starved larvae lay fewer eggs, but mature eggs from flies of widely differing sizes vary little in size and weight. The number of eggs laid per batch provides a good indication of the number of ovarioles present. There is no evidence of resorption of eggs retained in the ovaries, but the eggs are no longer viable after 17 days, and histological examination shows that breakdown of the eggs has taken place.

I. Introduction

In a study of *Lucilia cuprina* (Wied.) in the field it would be of material assistance to know the potential productivity of a blowfly population. Mackerras (1933) and Ullyett (1950) have pointed out that the fecundity of a fly is dependent on its size, and it is generally true for insects that restriction of larval food results in the production of undersized adults. The purpose of this paper is to place on a quantitative basis the relationships between the adequacy of larval food, the weight of puparia, the size of adults, and the reproductive capacity of adults. Also of importance in field studies is the question whether eggs remain viable if they are retained for extended periods within the fly's ovarioles due to the absence of sites capable of stimulating the oviposition response.

II. Methods

Eggs were collected on liver slices placed in cages containing gravid *L. cuprina* females. Immediately after hatching varying numbers of young larvae were placed on a standard quantity (10 g) of homogenized sheep brain in an incubator at 30°C and 20 per cent. relative humidity. The homogenized brain was placed in a small jar and covered, but not sealed, by a sheet of glass resting on two small wooden supports. This prevented the medium from drying out too rapidly. This jar was placed in a maggot-proof tray (Fuller 1934) the bottom of which was covered by finely chopped balsa wood, a material which provides suitable conditions for pupation and which, unlike sand, does not adhere to the larvae and so interfere with weighing (Nicholson, unpublished data).

* Division of Entomology, C.S.I.R.O., Canberra, A.C.T.

The puparia were weighed on a torsion balance about 12 hr before emergence and placed separately in glass vials to emerge. Pairs of flies were selected from puparia of approximately equal weight. Each pair was placed in a jar measuring 4 × 4 in. and 6 in. high. Sugar was available on the floor and water and liver were provided in two small separate jars.

After dissection the ovaries were stained with acetic-orcein to facilitate the counting of ovarioles.

Adult thoracic length was measured from the anterior margin of the prothorax to the posterior point of the scutellum, the fly being viewed laterally.

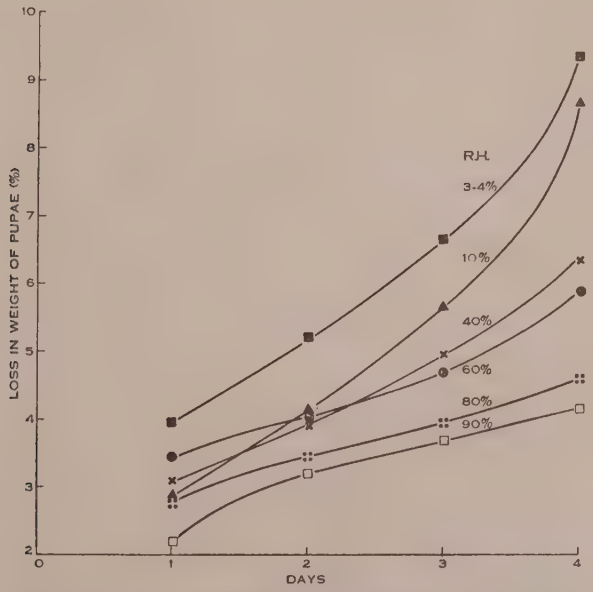


Fig. 1.—Mean percentage loss of weight of puparia during the pupal period at different relative humidities.

III. Results

(a) *Loss of Weight During Pupal Period*

Ullyett (1950) noted that during the pupal period of *L. sericata* (Meig.), there was a considerable loss of weight which varied with humidity. To determine whether this occurred in *L. cuprina*, batches of 20 puparia held at six different relative humidities (obtained with KOH solutions (Buxton 1931)), were used to determine the loss of weight during the pupal period. Figure 1 shows that during the pupal period there was an important loss of weight and that this varied with humidity. Consequently, in the following experiments, the puparia were kept at a

constant relative humidity and temperature (20 per cent. R.H. and 30°C respectively), and weighed about 12 hr before emergence.

(*b*) *The Relationship between Puparial Weight and Amount of Food Provided per Larva*

Figure 2 shows the relationship between the number of larvae per 10 g of food and the average weight of resulting puparia. The four points on the graph (each an average of about 40 puparia) confirm data obtained by Dr. A. J. Nicholson (personal communication).

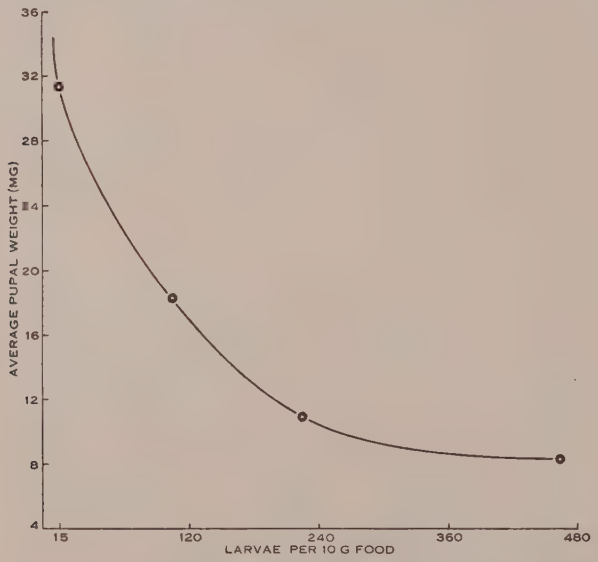


Fig. 2.—Relationship between puparial weight and the amount of food provided per larva.

Larval mortality was negligible for the lower 2 degrees of crowding but increased steeply thereafter. Restriction of larval food therefore resulted first in the production of puparia smaller in size rather than a smaller number of puparia, and later both in mortality and in reduction in pupal size. The range of variation in weight from the most crowded to the least crowded conditions was four-fold.

(*c*) *The Relationship between Puparial Weight* (X), *Length of Thorax* (Y), *and Number of Ovarioles* (Z)

By progressively increasing the number of larvae placed on successive standard amounts (10 g) of homogenized brain it was possible to obtain puparia varying in weight from 35.2 mg (15 larvae) to 6.3 mg (480 larvae). The resulting female flies were fed for 3 days on liver slices and the number of ovarioles counted after dissection. Figure 3 shows the

relationship between puparial weight and thoracic length, and Figure 4 the relationship between puparial weight and number of ovarioles. The largest females (puparia 33-35 mg) had an average of 230 ovarioles and the smallest (puparia 6-8 mg) an average of 70 ovarioles. The relationship between thoracic length and number of ovarioles is shown in Figure 5.

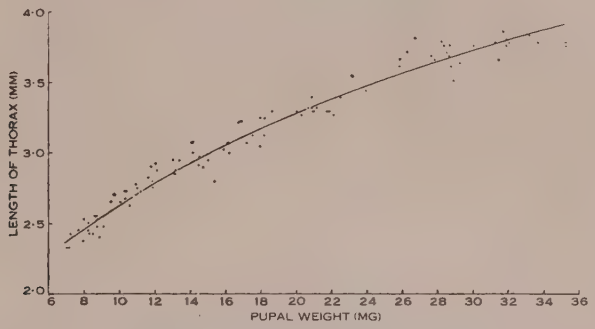


Fig. 3.—Relationship between puparial weight and length of thorax of adult female *L. cuprina*.

Curves of the form

$$Y = aX^b,$$

where a and b are constants, were fitted to the data. The equations of the curves (Figs. 3-5) are:

$$Y = 2.53\,X^{0.32},$$
$$Z = 15.80\,X^{0.78},$$
$$Z = 1.81\,Y^{2.39}.$$

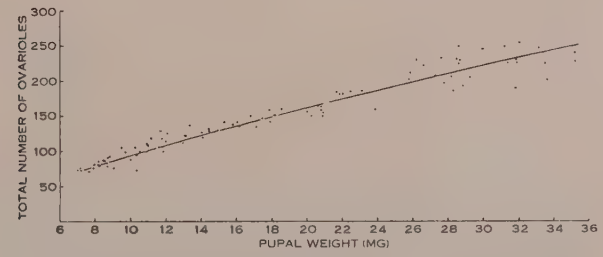


Fig. 4.—Relationship between puparial weight and number of ovarioles of adult female *L. cuprina*.

These data provide a basis from which it would be possible to assess the maximum reproductive capacity of flies caught in the field in traps. Also, from an examination of the size distribution of trapped flies, some estimate of the degree of competition for food to which larvae had been subjected in their breeding sites could be obtained.

(d) The Relationship between Puparial Weight and Length and Weight of Eggs

(i) *Egg Length.*—No difference could be detected in the length of eggs produced by flies emerging from puparia of average weight 7 mg (average number of ovarioles 75) and flies from puparia of average weight 35 mg (average number of ovarioles 235). This is illustrated in Figure 6 in which each point on the graph is an average of 20 readings.

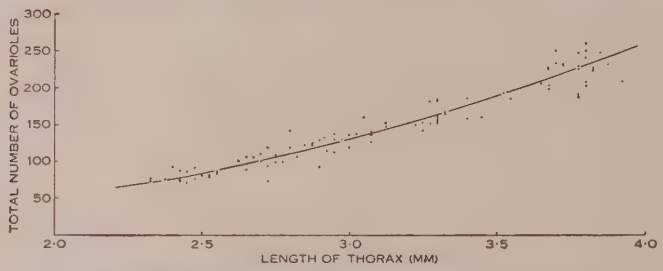


Fig. 5.—Relationship between length of thorax and number of ovarioles of adult female *L. cuprina.*

The data obtained were classified according to puparial weight into four classes and the mean and variance of corresponding egg lengths calculated. There was no evidence of any tendency for the egg length to change with puparial weight.

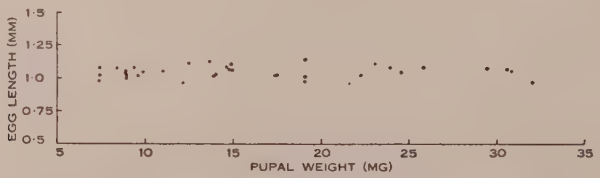


Fig. 6.—Relationship between puparial weight and length of eggs produced by adult female *L. cuprina.*

(ii) *Egg Weight.*—No differences were observed in the average weight of eggs from flies of different sizes (Fig. 7). There is some scatter which is possibly due in part to the fact that the eggs were weighed at times varying up to 3 hr after oviposition. This explanation is suggested since it was found that at a relative humidity of approximately 38 per cent. eggs lost up to 13 per cent. of their weight in 4 hr. Thus, even an hour's delay in weighing would involve some reduction in average weight.

(e) Egg Production in Relation to Number of Ovarioles

Under laboratory conditions with adequate food, young fertile females produced batches of mature eggs at 48-hr intervals. In Table 1 are shown the number of eggs laid per oviposition by a series of flies of varying size.

This is correlated with the number of ovarioles in each case, the latter having been determined by dissection at the end of the experiment. It is apparent that most, in some cases all, of the ovarioles function at oviposition, and there was no obvious effect of size on the ability of the fly's ovarioles to produce eggs.

Dissection of individuals in which the number of eggs laid was less than the number of ovarioles showed that this deficiency was not due to the retention of mature eggs in the ovarioles. It can therefore be seen that the egg counts recorded indicate, as far as can be ascertained, the number of ovarioles functioning at the particular period of egg maturation. Ovarioles that had failed to ovulate at an earlier oviposition (see Table 1, flies No. 1, 3, 8, and 11) were capable of ovulating at a later stage. The reasons underlying this failure to ovulate are not at present known.

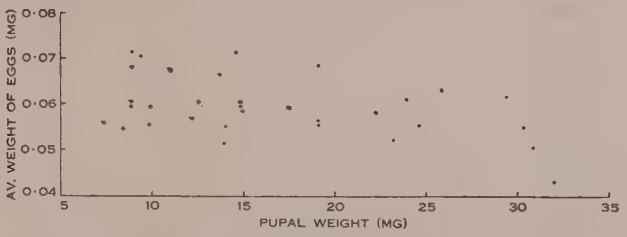


Fig. 7.—Relationship between puparial weight and the mean weight of single eggs produced by adult female *L. cuprina*.

(*f*) *Ovulation in Virgin Females*

Virgin females very rarely lay eggs. However, there is good evidence that their eggs mature normally, for flies fed continuously on liver for 8 days after emergence have been found on dissection to have as many as three eggs in each ovariole. Had these females been fertile they would have produced three batches of eggs. It can thus be seen that ovulation can continue in the absence of oviposition.

(*g*) *Effect of Adequate Food for Progeny of Small Flies*

To observe if starvation of larvae produced any hereditary effects, larvae from eggs of small flies (puparial weights 6.5-11.8 mg) were given adequate food. The resulting flies (puparial weights 29.3-34.7 mg) were of normal size and had a normal number of ovarioles (210-250, average 230).

(*h*) *Resorption of Eggs*

Females fed on liver, sugar, and water for 3 days after emergence develop one batch of eggs. To determine whether there was any resorption of unlaid eggs newly emerged, fertile females were fed on liver, sugar, and water for 3 days and then on sugar and water only for periods up to 32 days. At the end of 8, 14, 17, 21, and 28 days after emergence liver

was placed in the jars. Males were also added. Oviposition and viability were normal at 8 days, showing that resorption had not occurred. After this time, however, laying became more spasmodic and viability of the eggs decreased, none of the eggs being viable after about 17 days. Histological examination showed that visible breakdown of the eggs in the ovarioles was occurring from 14 days onwards.

TABLE 1

EGG PRODUCTION IN RELATION TO NUMBER OF OVARIOLES IN L. CUPRINA

Flies fed on liver for 6 hr each day. Each batch laid at 48-hr intervals

Fly No.	Pupal Weight (mg)	No. of Ovarioles	No. of Eggs			
			1st Batch	2nd Batch	3rd Batch	4th Batch
1	6.30	62	62	59	23	57
2	7.91	76	73	61	60	
3	8.20	81	75	80		
4	8.25	80	80	78		
5	8.65	83	83			
6	9.48	105	105			
7	16.08	142	139			
8	18.15	152	111	143	137	129
9	21.70	184	153			
10	23.12	186	178			
11	21.88	182	125	176		
12	26.20	230	226			
13	28.82	193	183	152		
14	32.00	260	257	238		

IV. Discussion

It is evident that there is a very close correlation between adequacy of larval food, puparial weight, and number of ovarioles of the adult female. There is no apparent change in external morphology for the undernourished pupa appears to produce a small replica of a normal adult. Restriction of larval food results in the production of undersized puparia from which emerge small-sized adults having ovaries with a reduced number of ovarioles, capable of producing a series of normal-sized viable eggs.

In some insects (certain pteromalids (Flanders 1935), *Schistocerca gregaria* (Roonwal 1946), *Habrobracon* (Grosch 1950), *Mormoniella vitripennis* (Edwards 1954)) resorption of undeposited eggs has been reported. There is no evidence that this occurs in *L. cuprina*, although eggs retained in the ovaries for a protracted period show some degenerative changes, and are no longer viable.

V. Acknowledgments

The author wishes to acknowledge the advice and encouragement of Dr. D. F. Waterhouse during the course of this investigation. Thanks are also due to Mr. G. A. McIntyre for the statistical analysis.

VI. References

Buxton, P. A. (1931).—The measurement and control of atmospheric humidity in relation to entomological problems. *Bull. Ent. Res.* **22**: 431-47.

Edwards, R. L. (1954).—The effect of diet on egg maturation and resorption in *Mormoniella vitripennis* (Hymenoptera, Pteromalidae). *Quart. J. Micr. Sci.* **95**: 459-68.

Flanders, S. E. (1935).—An apparent correlation between the feeding habits of certain pteromalids and the condition of their ovarian follicles. *Ann. Ent. Soc. Amer.* 28: 438-44.

Fuller, M. E. (1934).—The insect inhabitants of carrion: a study in animal ecology. Coun. Sci. Industr. Res. Aust. Bull. No. 82.

Grosch, D. S. (1950).—Starvation studies with the parasitic wasp *Habrobracon*. *Biol. Bull. Wood's Hole* **99**: 65-73.

Mackerras, M. J. (1933).—Observations in the life-histories, nutritional requirements, and fecundity of blowflies. *Bull. Ent. Res.* **24**: 353-62.

Roonwal, M. L. (1946).—On variation in the number of ovarioles and its probable origin in the desert locust *Schistocerca gregaria* (F). *Rec. Indian Mus.* **44**: 375-84.

Ullyett, G. C. (1950).—Competition for food and allied phenomena in sheep blowfly populations. *Phil. Trans.* B **234**: 77-174.

FURTHER AUSTRALIAN HARVESTMEN (ARACHNIDA: OPILIONES)

By R. R. Forster*

(*Manuscript received February 7, 1955*)

Contents

Summary

In the present paper 20 new species and five new genera are added to the Australian harvestman fauna. Examination of the type material of some of the previously described species has permitted a number of these to be redescribed and figured.

Introduction

Of the 20 new species described in the present paper, three are of particular interest. The record of a species of *Rakaia* Hirst from Queensland constitutes the first record of the suborder Cyphophthalmi from Australia, while the occurrence of *Austropsopilio novaehollandiae*, gen. et sp. nov. in Queensland extends the range of the family Acropsopilionidae, which has been previously recorded from South America, South Africa, and New Zealand. These two records in conjunction with the numerous endemic triaenonychids which have been recorded are considered by the present author to represent elements of an early Australian fauna which is closely related to the present New Zealand fauna. By contrast, *Austribalonius horridus*, gen. et sp. nov., is closely related to *Metibalonius* spp. from New Guinea. This species, with the remainder of the Australian phalangodids and the assamiids, is considered by the present author to represent a comparatively recent faunal influx into Australia from the north. Although at present too little is known of the Australian fauna to permit any definite conclusions to be drawn, it would appear that the dominant element of the southern portion of Australia, and particularly

* Canterbury Museum, Christchurch, New Zealand.

of the south-eastern region, consists of triaenonychids, whereas to the north, particularly in northern Queensland, this family is largely replaced by phalangodids and assamiids. It is of interest to note the absence of both phalangodids and assamiids from Tasmania, although this apparent absence may be due to the paucity of our knowledge of the fauna of this area.

The terminology used in the descriptions given below is outlined in an earlier paper on New Zealand harvestmen (Forster 1954). The following abbreviations have been used to indicate the present location of material studied: A.M. Australian Museum, Sydney; C.M. Canterbury Museum, Christchurch, N.Z.; N.M. National Museum of Victoria; Q.M. Queensland Museum, Brisbane; U.Q. Entomology Department, University of Queensland, Brisbane.

Order **OPILIONES**
Suborder **CYPHOPHTHALMI** Simon
Family **SIRONIDAE** Simon
Subfamily **SIRONINAE** Hansen & Soerensen
Genus RAKAIA Hirst

RAKAIA WOODWARDI, sp. nov.

Figs. 1-7

Holotype Male

MEASUREMENTS (mm)

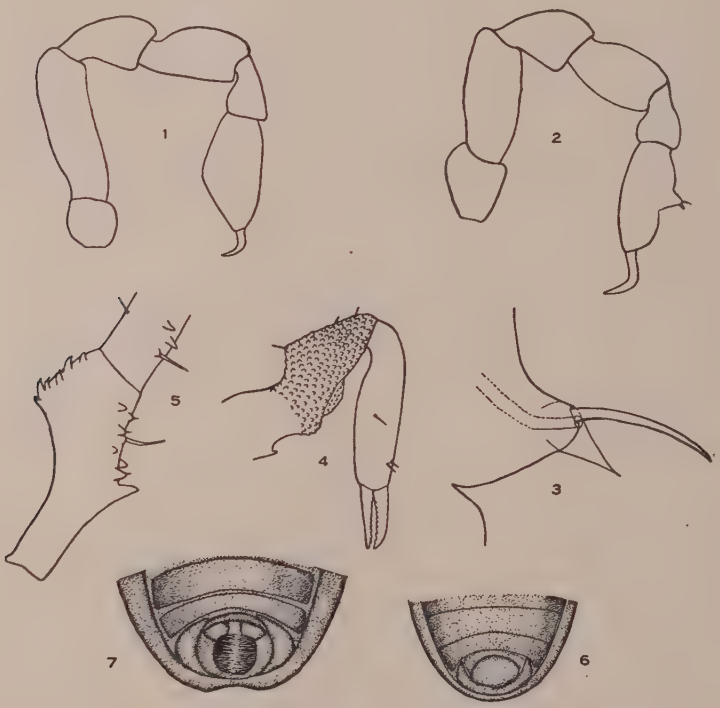
Body: length 1.76, width 1.19

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.44	0.15	0.53	0.31	0.39	0.22	0.35	2.39
Leg 2	0.39	0.13	0.44	0.18	0.31	0.13	0.34	1.92
Leg 3	0.38	0.13	0.31	0.22	0.29	0.18	0.29	1.80
Leg 4	0.57	0.22	0.39	0.23	0.35	0.19	0.35	2.30
Pedipalp		0.29	0.28	0.18	0.25		0.27	1.27
			Chelicera: basal 0.62, second 0.71					1.33

Colour: Entire animal dark reddish brown.

Body: Short and squat, entire surface evenly and finely granulate. Eyes absent. Cephalathorax widening posteriorly, where it is slightly wider than the abdomen. Scent gland mounds bluntly conical, sloping more steeply posteriorly, wider than high in the ratio of 7: 6; set a distance equal to one-half of their diameter from the lateral margins of the carapace and four and a half times their diameter apart. Tergites clearly defined by straight transverse grooves. Median groove extending down all tergites, broader on tergite 8 which, however, does not possess any lateral lobes or scopulae. Corona analis as in Figure 7. Anal plate provided with a pair of slightly distended areas near the anterior margin and with a thick median scopula. Abdomen not flexed down posteriorly. Arculi genitales broad, directed in from the lateral margins of the genital opening but not meeting anteriorly. Stomotheca longer than wide in the ratio of 6: 4.

Chelicerae (*Fig. 4*) : Basal segment strongly granulate. Dorsal ridge low and somewhat rounded. There are 2 low ventral swellings. Second segment not granulate. Teeth on inner surfaces of fingers are as shown in Figure 4.



Figs. 1-7.—*Rakaia woodwardi*, sp. nov.
Fig. 1, leg 1 of male; Fig. 2, leg 4 of male; Fig. 3, tarsal spur of male; Fig. 4, male chelicera; Fig. 5, trochanter and base of femur of male pedipalp; Fig. 6, distoventral surface of abdomen of female showing corona analis; Fig. 7, ditto of male.

Pedipalps (*Fig. 5*) : Trochanter with a strong ventral process at midway and a number of small spinous tubercles on both dorsal and ventral surfaces of the distal half of the segment. There are a few denticulations on the ventral surface of the femur.

Legs (*Figs. 1-3*) : All segments other than tarsi strongly granulate. Tarsal claws smooth. Tarsus 4 as in Figure 3. The dorsal spur is subconical, with the anterior margin much longer than the posterior, and provided with a translucent pyriform plate extending above the apex but inserted on the prolateral surface. The opening of the tarsal gland is from the apex of the spur near the base of a strong seta.

Allotype Female

MEASUREMENTS (mm)

Scute: length 2.07, width 1.24

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.44	0.18	0.48	0.22	0.35	0.18	0.38	2.23
Leg 2	0.39	0.18	0.39	0.20	0.27	0.17	0.31	1.91
Leg 3	0.31	0.15	0.31	0.21	0.27	0.18	0.27	1.70
Leg 4	0.48	0.22	0.40	0.21	0.31	0.19	0.31	2.12
Pedipalp		0.27	0.29	0.18	0.22		0.27	1.23
Chelicera: basal 0.79, second 0.83								1.62

Similar in general structure to male. The median groove is faint and limited to the first 5 tergites. Corona analis as in Figure 6. The arculi genitales are subtriangular and project over the posterior corners of the genital opening. Stomotheca longer than wide in ratio of 10: 9.

Types.—Holotype ♂ and allotype ♀, Clump Point, north Queensland, ex leafmould (3.vi.1953, T. E. Woodward) (Q.M.); paratypes, same data (A.M., C.M., and U.Q.).

Specimens examined.—Tully Falls, Queensland (21.viii.1953, W. A. McDougall), 1 ♀ (C.M.).

Remarks.—The species described above is the first cyphophthalmid to be recorded from Australia. The occurrence of this suborder in Australia is not surprising but it is of some interest to note the close relationship this species shows with the New Zealand fauna. It might be expected that relationship would be shown with the tropical representatives of the suborder as the predominant opiliones of northern Queensland, the phalangodids and assamiids, have northern affinities. *Rakaia woodwardi* is readily separated from all New Zealand species of this genus by the shape of the tarsal spur of the 4th leg of the male and the form of the anal plate.

Suborder **PALPATORES** Thorell
Family **ACROPSOPILIONIDAE** Roewer
Genus AUSTROPSOPILIO, gen. nov.

Eyemound elongate, directed forward, eyes large. Abdominal tergites free. Sternites clearly defined by transverse grooves. Genital operculum large. Maxillary lobes of coxae 2 widely separated, directed across the body. Chelicerae short, teeth on fingers small and uniform. Pedipalps longer than body, all segments other than tarsus with prominent lobes, provided with simple black setae; tarsus slightly smaller than tibia, with terminal claw.

Genotype *Austropsopilio novaehollandiae,* sp. nov.

Austropsopilio, gen. nov., is clearly separated from the three previously recorded genera, *Acropsopilio* from South America, *Cadella* from South Africa, and *Zeopsopilio* from New Zealand, by the more slender and elongated eyemound. It appears to be more closely related to *Cadella* with which it has in common the strong lobes on the pedipalps.

Austropsopilio novaehollandiae, sp. nov.

Figs. 8-11

Holotype (*Immature Female*)

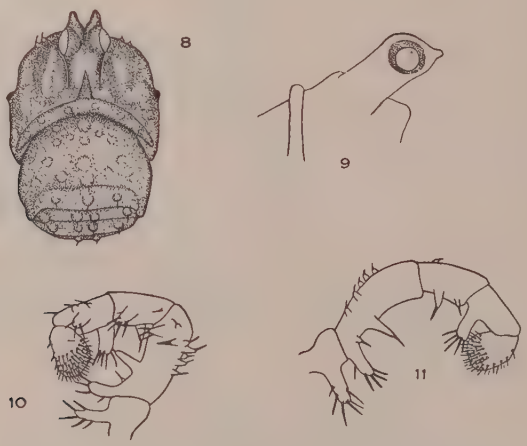
MEASUREMENTS (mm)

Scute: length 1.05, width 0.92

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.45	0.11	0.26	0.15	0.21	0.31	0.66	2.15
Leg 2	0.51	0.10	0.56	0.26	0.51	0.66	0.77	3.37
Leg 3	0.36	0.15	0.36	0.22	0.31	0.41	0.51	2.32
Leg 4	0.45	0.15	0.56	0.31	0.36	0.66	0.71	3.20
Pedipalp		0.18	0.32	0.30	0.22		0.20	1.22

Chelicera: basal 0.20, second 0.45 0.65

Colour: The ground colour of the body is pale yellow with numerous dark reddish brown markings. The eyemound is pale cream with black shading around the eyes. Pedipalps and legs with irregular bands of pale cream and brown.



Figs. 8-11.—*Austropsopilio novaehollandiae*, gen. et sp. nov.
Fig. 8, dorsal view of body; Fig. 9, lateral view of carapace and eyemound; Fig. 10, prolateral surface of pedipalp; Fig. 11, retrolateral surface of pedipalp.

Body: The eyemound is elongate (Figs. 8, 9) rising from well behind the anterior margin of the carapace and directed obliquely forward. The eyes are large and the area about them is distended leaving a median furrow. The distal portion of the eyemound is indented mesially leaving a pair of strong distal lobes. There are 2 small setose tubercles on the mid-lateral surfaces of anterior margin of the carapace. The openings of the scent glands are visible on the mid-lateral surfaces of the carapace. The carapace does not appear to be divided but there is a prominent ridge

along the posterior margin. The tergal region is fused, but without traces of segmentation. There are 3 free abdominal tergites. Both thoracic and abdominal tergal areas are provided with low rounded tubercles (Fig. 8). The genital operculum is extremely broad, its width is more than one-third the width of the abdomen, and is probably accentuated due to the immaturity of the specimen described. The maxillary lobes are suboval and are directed across the body.

Chelicerae: Small. Both segments are smooth. The inner margins of both fixed and moveable fingers are provided with small, black, even teeth.

Pedipalps (*Figs. 10, 11*) : There is a strong elongate tubercle on the ventral surface of the trochanter, provided with numerous smooth, black setae grouped mainly near the apex. There is a similar tubercle on the proximoventral surface of the femur. There is a strong conical tubercle with a single apical seta near the mid-ventral surface of the femur, two smaller tubercles near the distal prolateral surface of which the more distal is provided with 3 apical setae and a group of 5 small tubercles of normal appearance on the dorsal surface at about two-thirds. Trochanter with a strong tubercle on both pro- and retrolateral surfaces, prolateral with 3-4 setae, retrolateral with a single apical seta. Tibia with multisetose tubercles on both pro- and retrolateral surfaces, retrolateral much stronger. The tarsus is broad, rather flattened, and slightly shorter than the tibia. The distal half of the segment is clothed with numerous short black setae, tarsal claw absent.

Legs: These are short, relatively stout, and smooth. There is a tubercle on the ventral surface of coxa, trochanter, and femur of leg 1 and proximodorsal surface of metatarsus of all legs. Tarsal formula 7, 10-11, 8, 8.

Types.—Holotype (imm. female), Mt. Hobwee, Lamington Plateau, south Queensland, ex leafmould (27.viii.1953, T. E. Woodward) (Q.M.).

Suborder **LANIATORES** Thorell
Family **ASSAMIIDAE** Soerensen
Subfamily **DAMPETRINAE** Roewer
Genus DAMPETRUS Karsch
DAMPETRUS AUSTRALIS Karsch
Figs. 12-14

Dampetrus australis Karsch (pt.), 1880, Z. Naturw. 53: 403.
Dampetrus fuscus Soerensen, 1886, Arach. Austral. 2: 80.
Dampetrus tuberculatus Soerensen, 1886, Arach. Austral. 2: 82.
Dampetrus tuberculatus Roewer, 1912, Arch. Naturgesch. 78A: 16.
Dampetrus fuscus Roewer, 1912, Arch. Naturgesch. 78A: 16.
Dampetrus tuberculatus Roewer, 1920, Ark. Zool. 13: 2.
Dampetrus fuscus Roewer, 1920, Ark. Zool. 13: 2.
Dampetrus australis Roewer, 1923, Die Weberknechte der Erde, Jena, 222.
Dampetrus tuberculatus Roewer, 1923, Die Weberknechte der Erde, Jena, 222.
Dampetrus fuscus Roewer, 1923, Die Weberknechte der Erde, Jena, 223.

This species appears to be one of the most common of the Australian assamiids. An examination of Karsch's type material of *D. australis* indicates that the two specimens he examined are both females, although their brittle nature, due to long preservation, has not permitted an examination of the genitalia. They represent two distinct species. The specimen selected below as lectotype is identical with *D. tuberculatus* Soerensen and *D. fuscus* Soerensen. The type specimens of these 2 species have been available for examination. Karsch's second specimen is identical with the species described by Soerensen as *D. granulatus* and is placed into the synonymy of this species.

Female

MEASUREMENTS (mm)

Lectotype ♀

Carapace: length 3.75, width 2.20

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	1.15	0.32	1.99	0.62	1.27	—	—	—
Leg 2	1.27	0.44	3.35	0.88	3.08	—	—	—
Leg 3	1.22	0.48	2.68	—	—	—	—	—
Leg 4	1.91	0.66	3.52	0.67	2.29	3.74	1.48	14.27
Pedipalp		0.48	1.15	0.53	0.67	—	0.50	3.33
		Chelicera: basal 0.88, second 1.32						2.20

Female (Herberton)

Carapace: length 2.86, width 2.03

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.92	0.32	1.98	0.66	1.36	2.47	1.06	8.77
Leg 2	1.28	0.44	3.56	0.84	3.17	3.96	2.03	15.28
Leg 3	1.25	0.48	2.68	0.84	1.76	3.08	1.32	11.41
Leg 4	1.76	0.62	3.96	0.79	2.42	4.40	1.62	15.57
Pedipalp		0.44	0.97	0.62	0.53	—	0.44	3.00
		Chelicera: basal 0.88, second 1.32						2.20

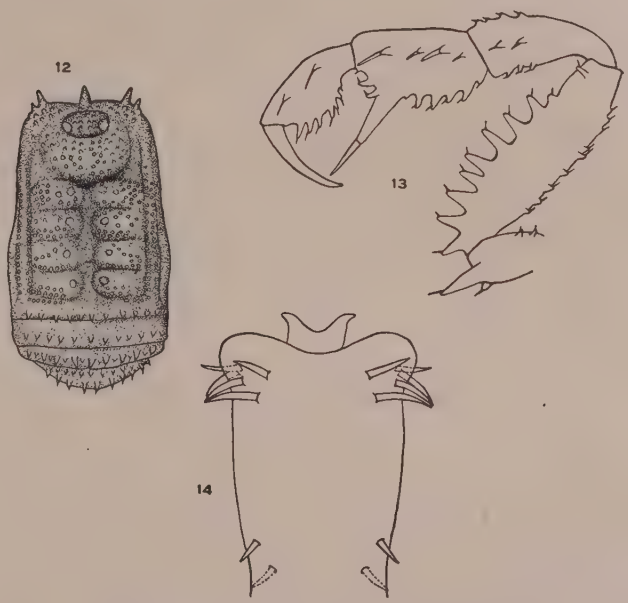
Lectotype Female

Colour: Uniform pale brown, with a few dark reticulate markings on the carapace.

Body (*Fig. 12*) : The eyemound is granulate, broad, twice as wide as long, width equal to two-sevenths the width of the carapace. The lateral margins of the scute are almost parallel. Scutal groove deep and well defined. Carapace granulate. Tergal areas clearly defined by transverse grooves, with a pronounced median longitudinal furrow. Areas 1-4 are granulate, with a more prominent tubercle on the slightly swollen areas each side of the median depression. There is a ridge down each lateral margin of the scute which is provided with 2 longitudinal rows of small granules.

Chelicerae: Basal segment swollen on distodorsal surface which is strongly granulate. Second segment smooth apart from a few low setose tubercles, situated mainly on the dorsal surface.

Pedipalps (*Fig. 13*) : The pedipalps of all species of this genus appear to be very similar. There is a strong spinous tubercle on the ventral surface of the trochanter and a row of 9-10 similar tubercles along the



Figs. 12-14.—*Dampetrus australis* Karsch.
Fig. 12, dorsal view of body of female; Fig. 13, prolateral surface of pedipalp of female; Fig. 14, male genitalia.

ventral surface of the femur and a smaller tubercle on the distal prolateral surface. The tibia is armed with a strong spinous tubercle on the subdistal retroventral margin.

Legs: These are finely granulate, lacking processes. The tarsal formula is somewhat variable, the recorded range is as follows: 6-8, 10-14, 6-7, 6-8. The distotarsal count of the 1st and 2nd legs of specimens examined by the present author is 3.

Male

MEASUREMENTS (mm)

Scute: length 3.74, width 2.64

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.97	0.44	2.51	0.85	1.85	3.08	1.32	11.02
Leg 2	1.32	0.44	4.49	0.97	3.79	4.62	2.59	18.22
Leg 3	1.32	0.66	3.21	1.01	2.03	3.56	1.45	13.24
Leg 4	2.86	0.66	4.62	1.32	3.08	4.85	1.76	19.15
Pedipalp		0.44	1.32	0.57	0.57	—	0.48	3.38
			Chelicera: basal 1.15, second 1.76					2.91

The scute and eyemound are similar to female. The 2nd segment of the chelicera is more distended, the diameter at the widest portion is equal

to four-tenths the length of the segment. The 4th pair of coxae are more strongly developed, being 3 times as long as the 1st pair of coxae. The femur and patella of the 4th pair of legs are stronger than in female and are coarsely granulate. The genitalia are slender and the distal portion is shown in Figure 14.

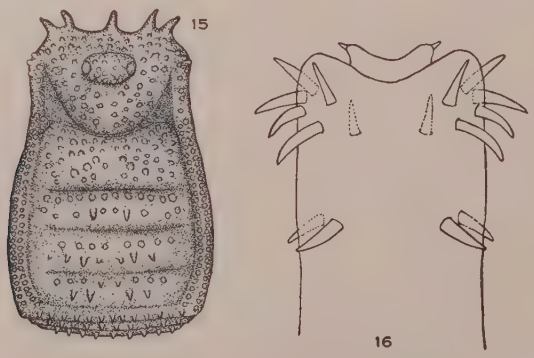
Types.—Lectotype female, Western Australia, in Berlin Museum, syntype female = *Dampetrus granulatus* Soerensen, in Berlin Museum (seen).

Specimens examined.—QUEENSLAND: Port Mackay 3 ♀ ♀ (described as *D. fuscus* by Soerensen), in Hamburg Museum; Herberton (Id. *D. tuberculatus* Soer. by Roewer 1920), in Stockholm Museum; Malanda (Id. *D. granulatus* Soer. by Roewer 1920), in Stockholm Museum; Herberton (Id. *D. fuscus* Soer. by Roewer 1920), in Stockholm Museum; Eidsvold (A.M. No. K30722); Albert River, near Hillview (8.iv.1939), under logs in damp situations (U.Q. No. K3); Caloundra (Aug. 1939), 6 ♀ ♀ (U.Q.).

DAMPETRUS GRANULATUS Soerensen

Figs. 15, 16

Dampetrus granulatus Soerensen, 1886, Arach. Austral. 2: 82.
Dampetrus australis Karsch (pt.), 1880, Z. Naturw. 53: 403.
Dampetrus cristatus Soerensen, 1886, Arach. Austral. 2: 83.
Dampetrus granulatus Roewer, 1912, Arch. Naturgesch. 78A: 16.
Dampetrus cristatus Roewer, 1912, Arch. Naturgesch. 78A: 17.
Dampetrus granulatus Roewer, 1920, Ark. Zool. 13: 2.
Dampetrus granulatus Roewer, 1923, Die Weberknechte der Erde Jena, 222.
Dampetrus cristatus Roewer, 1923, Die Weberknechte der Erde Jena, 223.



Figs. 15, 16.—*Dampetrus granulatus* Soerensen. Fig. 15, dorsal view of body of male; Fig. 16, male genitalia.

This species has been confused with *D. australis* Karsch but it is clearly separated from it by the absence of a median tergal groove and more strongly developed anterolateral spines (Fig. 15).

The male genitalia of the two species are similar in appearance but the setae of *granulatus* are relatively stronger, with the 2 posterior pairs situated much closer to the anterior setae (Fig. 16).

An examination of Soerensen's type material has shown that *D. cristatus* Soer. is synonymous with *D. granulatus* Soer.

Types.—Thirteen syntypes of *D. granulatus* Soer., Rockhampton, Qld., in Hamburg Museum; 4 syntypes of *D. cristatus* Soer., Sydney, N.S.W., in Hamburg Museum; syntype ♀ of *D. australis* Karsch, Western Australia, in Berlin Museum (seen).

Specimens examined.—Herberton, Queensland (det. Roewer 1927) in Stockholm Museum; Bogan River, New South Wales, on Myall ground (9.ix.1952, J. W. T. Armstrong), 2 ♂♂, 3 ♀♀ (A.M. and C.M.).

Dampetrus geniculatus Soerensen

Figs. 17-19

Dampetrus geniculatus Soerensen, 1886, Arach. Austral. 2: 81.
Dampetrus geniculatus Roewer, 1912, Arch. Naturgesch. 78A: 16.
Dampetrus geniculatus Roewer, 1920, Ark. Zool. 13: 2.
Dampetrus geniculatus Roewer, 1923, Die Weberknechte der Erde Jena, 222.

The type specimen of this species cannot be found and has apparently been lost during the wartime storage of the collections of the Hamburg Museum. I have been permitted to examine the specimen held in the Stockholm Museum, identified by Roewer in 1920 as this species, and have used this specimen for the description and figures given below.

Male

MEASUREMENTS (mm)

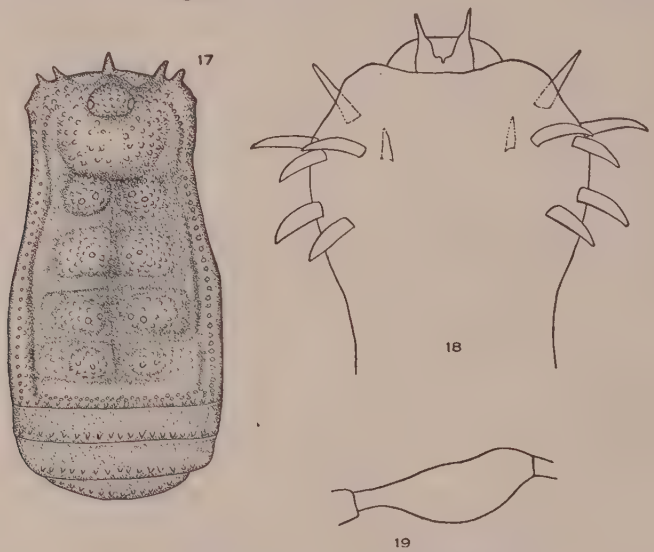
Scute: length 4.85, width 3.08

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	1.32	0.62	2.64	0.92	2.03	3.35	1.42	12.30
Leg 2	1.76	0.71	4.98	1.32	4.49	5.06	3.20	21.52
Leg 4	1.54	0.75	3.30	1.00	2.52	3.74	2.03	14.88
Leg 3	3.52	0.88	3.52	1.40	3.51	3.96	2.36	19.15
Pedipalps		0.61	1.52	0.88	1.00		0.88	4.89
			Chelicera: basal 1.32, second 1.76					3.08

Colour: The body and appendages are uniform yellowish brown.

Body (*Fig. 17*): The eyemound is uniformly granulate, wider than it is long in the ratio of 3: 2 and removed from the anterior margin of the carapace by a distance equal to one-half its length. The carapace is sparsely granulate, much lower than the tergal region and separated from it by a deep scutal groove. The tergal areas are defined by broad, shallow grooves. Areas 1-4 each with a low swelling on each side of the median line. The swellings are granulate and each has a pair of larger, rather conspicuous granules. Lateral ridges are present. The posterior margin of the scute and the free tergites are each provided with a transverse row of small conical tubercles.

Genitalia: The distal portion of the penis is distended. There is a double spinous apical process present. The setae are strong and are arranged as shown in Figure 18.



Figs. 17-19.—*Dampetrus geniculatus* Soerensen.
Fig. 17, dorsal view of body of male; Fig. 18, male genitalia;
Fig. 19, femur of leg 4 of male.

The chelicerae and pedipalps are typical.

Legs: Finely granulate. Femur of the 4th leg is swollen, its greatest width is equal to one-quarter of the length of the segment (Fig. 19). The tarsal formula is 7-8, 13, 6, 7. The tarsal count of leg 1 differs between the 2 legs of the single specimen examined. The distotarsi of legs 1 and 2 is 3 and 4 respectively.

Type.—Gayndah, sex?, in Hamburg Museum (probably lost).

Specimen examined.—Atherton, Queensland, 1 ♂ (det. Roewer 1920), No. 4346, in Stockholm Museum.

Dampetrus soerenseni, sp. nov.
Figs. 20-22

Holotype Male

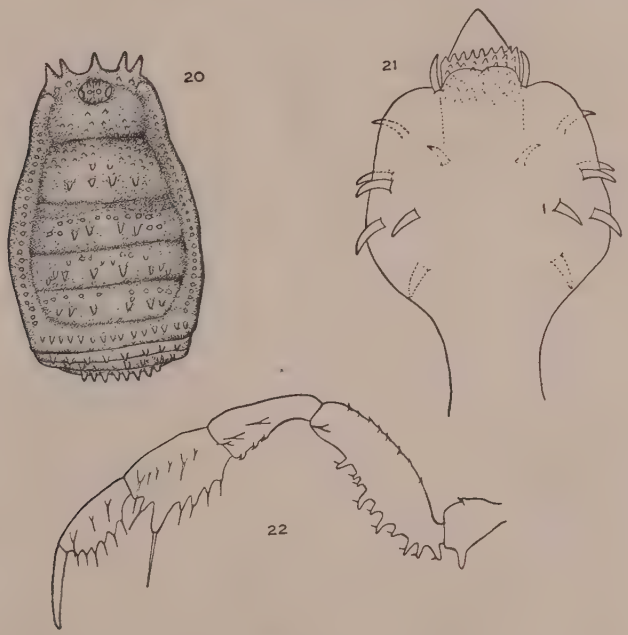
MEASUREMENTS (mm)

Scute: length 3.89, width 2.43

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.72	0.35	1.76	0.64	1.49	2.29	0.97	8.22
Leg 2	1.15	0.44	3.35	0.72	2.88	3.49	1.76	13.79
Leg 3	1.24	0.52	2.48	0.80	1.76	2.42	0.88	10.10
Leg 4	2.64	0.60	3.41	0.97	2.95	3.96	1.36	15.89
Pedipalp		0.39	0.76	0.48	0.44		0.39	2.46
			Chelicera: basal 0.48, second 0.88					1.36

Colour: The entire animal is heavily shaded with dark blackish brown but the trochanters of all legs are pale yellow.

Body (*Fig. 20*) : The eyemound is relatively small and low. It is twice as wide as it is long, with a shallow median longitudinal furrow, and a row of from 3 to 4 granules above each eye. Carapace sparsely granulate.



Figs. 20-22.—*Dampetrus soerenseni*, sp. nov.
Fig. 20, dorsal view of body of male; Fig. 21, male genitalia;
Fig. 22, prolateral surface of male pedipalp.

Scutal groove shallow but distinct. There is a well-defined lateral ridge with a double row of small granules. Tergal areas defined by shallow transverse grooves. Areas 1-4 with sharp conical tubercles, 4 on areas 1-3, but 6 on area 4. The tubercles on area 1 are situated near the posterior margin, anterior half strongly granulate. There are only few granules on the remaining areas. The posterior margin of the scute and free tergites with a transverse row of small, sharp tubercles. Genital operculum with few small granules.

Genitalia: The distal portion is distended and provided with strong but relatively short setae distributed as shown in Figure 21.

Chelicerae: Not modified.

Pedipalps: As shown in Figure 22.

Legs: Coxa, femur, patella, tibia, and metatarsus of leg 4 with strong, sharp granules. Legs otherwise finely granulate. Tarsal formula 6, 11-12, 6, 7. Distotarsi of legs 1 and 2 are 2 and 3 respectively.

Allotype Female

MEASUREMENTS (mm)

Scute: length 2.73, width 2.29

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.78	0.35	1.74	0.60	1.24	1.94	0.72	7.37
Leg 2	1.10	0.44	2.73	0.72	2.38	2.86	1.85	12.08
Leg 3	1.01	0.48	1.03	0.60	1.45	2.24	1.01	7.82
Leg 4	1.74	0.52	2.64	0.80	2.20	3.30	1.01	12.21
Pedipalps		0.39	0.76	0.48	0.44		0.39	2.46
			Chelicera: basal 0.48, second 0.80					1.28

Similar to male in general structure. Tarsal formula 5-6, 11-12, 5, 6. Distotarsi as in male. Fourth leg with strong sharp tubercles restricted to the coxae.

Types.—Holotype male, allotype female and paratype female, near Herberton, Qld, 2.vii.1931, A. Musgrave (A.M.).

Specimens examined.—Specimens in Stockholm Museum from Atherton, Cooktown, and Mt. Tambourine, Queensland (*D. tuberculatus*) (Id. Roewer 1920).

Remarks.—D. soerenseni, sp. nov., is similar to *D. granulatus* Soer. in general appearance but may be readily separated from it by the relatively short carapace, the smaller eyemound, and the different form of the male genitalia.

Genus METAMERMERIS Roewer

METAMERMERIS SPECULATOR Roewer

Figs. 23-26

Metamermeris speculator Roewer, 1920, Ark. Zool. 13: 3.
Metamermeris speculator Roewer, 1923, Die Weberknechte der Erde, Jena, 225.

I have reexamined the two syntype specimens from Atherton, Queensland, recorded as male and female by Roewer. Both specimens have a penis extruding from the genital opening. The pronounced elevation of the proximal portion of the 2nd segment of the chelicerae of 1 specimen can be explained as a manifestation of male dimorphism. Male dimorphism has been found by the present author (Forster 1954) to occur commonly among New Zealand triaenonychids and it is not surprising to find it occurring in the Assamiidae. Similar dimorphism is known to the author in the family Phalangodidae and will undoubtedly prove to be of common occurrence in other families when a wider use of the structure of the genitalia as a taxonomic character is adopted. The following descriptions are based on the syntype material, from Atherton, held in the Stockholm Museum.

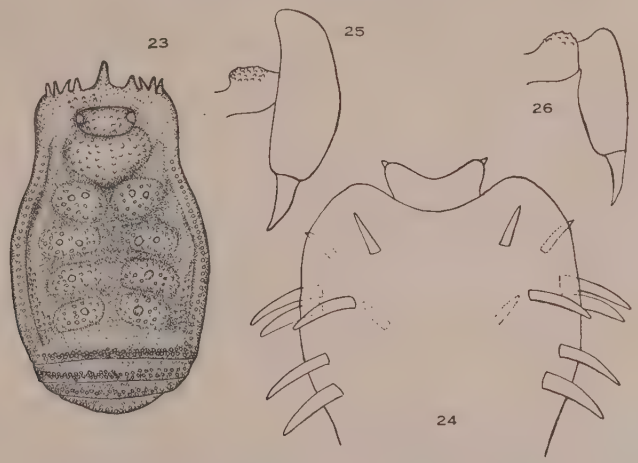
Form A *Male* (*Lectotype*)

MEASUREMENTS (mm)

Scute: length 3.96, width 3.12

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	1.32	0.66	1.76	0.75	1.54	2.54	1.32	9.89
Leg 2	1.76	0.61	3.39	0.88	2.86	3.52	2.91	15.93
Leg 3	1.71	0.71	2.64	0.89	1.98	3.08	1.54	12.55
Leg 4	2.64	0.79	3.71	1.23	2.20	3.76	1.81	16.14
Pedipalp		0.71	1.76	0.82	0.88		0.91	5.08

Chelicera: basal 0.88, second 3.08 3.96



Figs. 23-26.—*Metamermeris speculator* Roewer.
Fig. 23, dorsal surface of body of male; Fig. 24, male genitalia; Fig. 25, chelicera "form *A*" male; Fig. 26, chelicera "form *B*" male.

Body (*Fig. 23*): The eyemound is granulate, low and broad, width equal to three times length. Anterior margin of carapace with strong single median spine but with 4 smaller spines on each lateral margin. Carapace sparsely granulate. Scutal groove deep, lateral ridges well developed. Areas 1-4 with a slightly swollen granulate area on the mid-lateral surfaces with a pair of small tubercles on the first 2 areas but a single tubercle on areas 3 and 4. The posterior margin of the scute and the free tergites are provided with a transverse group of small pustules.

Genitalia: The penis is long and slender but the distal portion is distended. This region is provided with strong setae disposed as in Figure 24.

Chelicerae: The basal segment is constricted proximally and closely granulate on the distodorsal surface. The 2nd segment is massive and the proximal portion extends up well above the level of the basal segment (Fig. 25).

Pedipalps: These are similar in form to the pedipalps of *Dampetrus* spp. and show no unusual characters.

Legs: Normal. Tarsal formula 7, 14, 6, 7. Distotarsi of legs 1 and 2 is 3 and 4 respectively.

Form B *Male* (*Syntype*)

MEASUREMENTS (mm)

Scute: length 3.08, width 2.33

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	1.10	0.39	2.20	0.66	1.54	2.20	1.32	9.41
Leg 2	1.32	0.48	3.74	0.97	2.82	3.30	2.95	15.58
Leg 3	1.32	0.53	2.64	0.53	1.59	2.68	1.36	10.65
Leg 4	2.20	0.88	3.96	0.83	2.42	3.96	1.76	16.01
Pedipalp		0.57	1.36	0.81	0.71		0.48	3.93

Chelicera: basal 0.81, second 1.32 2.13

With the 2nd segment of the chelicera normal, not extending above the level of the basal segment (Fig. 26). Otherwise similar in structure to form *A* male.

Types.—Two male syntypes, Atherton, Qld, in Stockholm Museum. The form *A* male has been selected by the present author as lectotype.

Record.—Winton, Queensland, in Roewer collection (not examined).

Genus CARDWELLA Roewer 1935

CARDWELLA ATAR (Soerensen 1932)

Figs. 27-30

Wintonia atar Soerensen, 1932, Mem. Acad. Roy. Sci. Lettres, Copenhagen 9: 218.
Cardwella atar Roewer, 1935, Veroff. Dtsch. Kolon. Mus., Bremen 1: 63.

Syntype Male

MEASUREMENTS (mm)

Scute: length 3.08, width 2.20

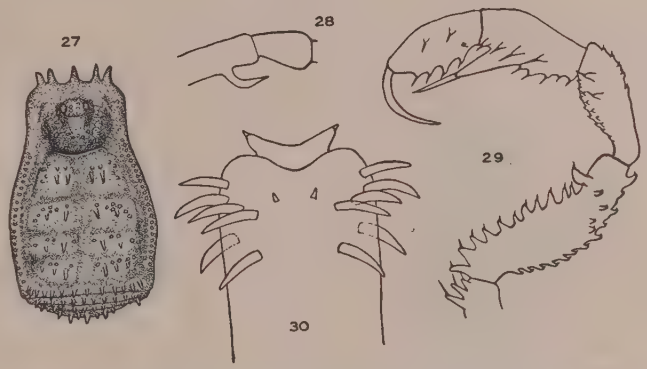
	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.88	0.31	1.76	0.57	1.32	2.38	0.88	8.10
Leg 2	1.10	0.39	3.08	0.79	2.51	3.61	1.98	13.46
Leg 3	1.01	0.44	2.42	0.75	1.54	2.91	1.10	10.17
Leg 4	2.33	0.48	4.40	1.01	2.47	4.85	1.32	16.86
Pedipalp		0.31	0.88	0.48	0.44		0.44	2.55

Chelicera: basal 0.53, second 1.01 1.54

Colour: The type specimens are pale yellowish brown, but fresh specimens amongst the material examined are dark brown.

Body (*Fig. 27*) : The eyemound is twice as wide as it is long, with 2 rows of granules. The carapace is low and only sparsely granulate. There are the usual 5 spines on the anterior margin of most of the specimens but some have 3, instead of 2 lateral spines. The scutal groove is deep, with the tergal region rising sharply from it. Tergal areas clearly defined by transverse grooves and with a shallow median furrow down areas 1-4. Areas 1-4 with 2 pairs of small conical tubercles in addition to a number of granules (Fig. 27). Lateral ridges well developed. Posterior margin of

the scute and free tergites each with a transverse row of small conical tubercles.



Figs. 27-30.—*Cardwella atar* (Soerensen).
Fig. 27, dorsal surface of body of male; Fig. 28, prolateral surface femur, leg 4 of male; Fig. 29, prolateral surface of male pedipalp; Fig. 30, male genitalia.

Genitalia (*Fig. 29*) : Slender, not distended distally, provided with 12 strong subdistal setae, arranged in 2 lateral groups of 6.

Chelicerae: Typical, basal segment strongly granulate on the disto-dorsal surface.

Legs: Femur of 4th leg with strong curved spinous process (Fig. 28) on the distoventral surface. The surface of the femur surrounding the process is strongly granulate and there are numerous elongate granules along the ventral surface of the tibia. The legs are otherwise finely granulate. Tarsal formula 5, 8-9, 5, 6. Distotarsi of legs 1 and 2 are 2 and 3 segmented respectively.

Syntype Female

MEASUREMENTS (mm)

Scute: length 2.64, width 1.89

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.88	0.31	1.32	0.44	0.92	1.50	0.75	6.12
Leg 2	1.06	0.30	2.24	0.66	1.81	2.38	1.32	9.77
Leg 3	0.92	0.35	1.89	0.65	1.10	1.76	0.66	7.33
Leg 4	1.32	0.39	2.29	0.68	1.41	2.43	0.83	9.35
Pedipalp		0.27	0.79	0.44	0.39		0.39	2.28
			Chelicera: basal 0.48, second 0.89					1.37

The female is very similar to the male in structure. The 4th femur lacks a spinous process and the 4th tibia is finely granulate. Tarsal formula 4, 8-10, 5, 6.

Types.—Syntypes, Cardwell, Qld, in Stockholm Museum (seen).

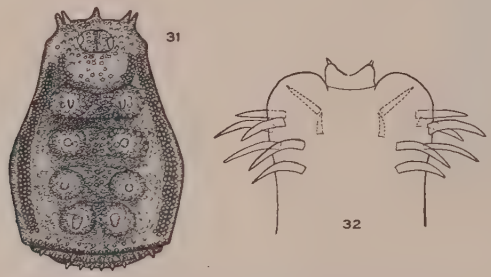
Specimens examined—Herberton, north Queensland, 1951, J. G. Brooks (A.M.).

Genus OCTOBUNUS Roewer

OCTOBUNUS SINGULARIS Roewer

Figs. 31, 32

Octobunus singularis Roewer, 1923, Die Weberknechte der Erde, Jena, 225.



Figs. 31, 32.—*Octobunus singularis* Roewer. Fig. 31, dorsal view of body of male; Fig. 32, male genitalia.

Male

MEASUREMENTS (mm)

Scute: length 3.08, width 2.33

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.64	0.44	2.47	0.64	1.59	3.08	1.41	10.27
Leg 2	0.80	0.48	4.85	0.88	3.96	4.85	2.20	18.02
Leg 3	1.10	0.52	2.95	0.68	1.94	3.36	1.80	12.35
Leg 4	2.64	0.64	4.40	0.88	2.88	4.87	2.02	18.33
Pedipalp		0.35	1.15	0.72	0.64		0.44	3.30
		Chelicera: basal 0.43, second 0.85						1.28

Colour: Body chelicerae and pedipalps dark brown, legs paler.

Body (*Fig. 31*): Eyemound low, almost twice as wide as it is long, sparsely granulate, with a shallow median longitudinal furrow. Carapace low and sparsely granulate. There is a strongly granulate ridge extending down the lateral margins of the scute. The scutal groove is deep and well defined. Tergal areas are defined by 4 broad transverse grooves. Areas 1-4 each with 2 strong conical swellings, which are strongly granulate and equal in height to the eyemound. Each swelling is provided with a definite apical tubercle. The posterior margin of the scute and the free tergites with small tubercles which are only slightly bigger than the granules. Genital operculum granulate.

Genitalia: Slender, not distended apically. Setae strong and grouped distally as shown in Figure 32.

Chelicerae and *pedipalps* are as described for *Dampetrus* spp.

Legs: Coxa 4, strongly granulate. Legs otherwise only finely granulate. Tarsal formula 7, 12, 6, 6-7. Distotarsi of legs 1 and 2 are 3 and 4 respectively.

Female

MEASUREMENTS (mm)

Scute: length 2.20, width 1.85

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.56	0.27	1.24	0.48	0.92	1.55	0.88	5.90
Leg 2	0.88	0.31	1.96	0.60	1.76	1.95	1.50	8.96
Leg 3	0.88	0.35	1.41	0.60	1.10	1.83	0.72	6.89
Leg 4	1.55	0.44	2.20	0.61	1.55	2.42	1.15	9.92
Pedipalps		0.22	0.68	0.44	0.39		0.31	2.04
			Chelicerae: basal 0.39, second 0.80					1.19

The female is less robust than the male, with the swellings on areas 1-4 virtually absent but represented by small tubercles. Tarsal formula 6, 9, 6, 7.

Types.—Holotype male, Winton, Qld, in Roewer collection in Bremen Museum (not seen).

Specimens examined.—QUEENSLAND: National Park (June 1939), 2 ♂♂, 2 ♀♀, 1 imm. (U.Q.); Brisbane (21.x.1942, I.F.B. Common), 3 ♀♀ (U.Q.); Natural Arch, Numinbar (Easter 1947, F. Bertie), 1 ♂ (U.Q.).

Family **PHALANGODIDAE** Simon
Subfamily **PHALANGODINAE** Roewer
Genus ZALMOXIS Soerensen 1886

ZALMOXIS CARDWELLENSIS, sp. nov.

Figs. 33-36

Holotype Male

MEASUREMENTS (mm)

Scute: length 2.86, width 1.91

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.62	0.22	0.88	0.39	0.56	1.06	0.66	4.39
Leg 2	0.75	0.27	1.32	0.53	1.15	1.54	1.11	6.67
Leg 3	0.66	0.31	1.01	0.44	0.88	1.32	0.66	5.28
Leg 4	1.01	0.48	1.59	1.45	0.71	1.76	0.88	7.88
Pedipalp		0.22	0.75	0.22	0.48		0.44	2.11
			Chelicera: basal 0.48, second 0.75					1.23

Colour: Carapace with black reticulate markings. Tergal region, free tergites and sternites heavily shaded with black. Pedipalps, chelicerae, and legs with black reticulate markings.

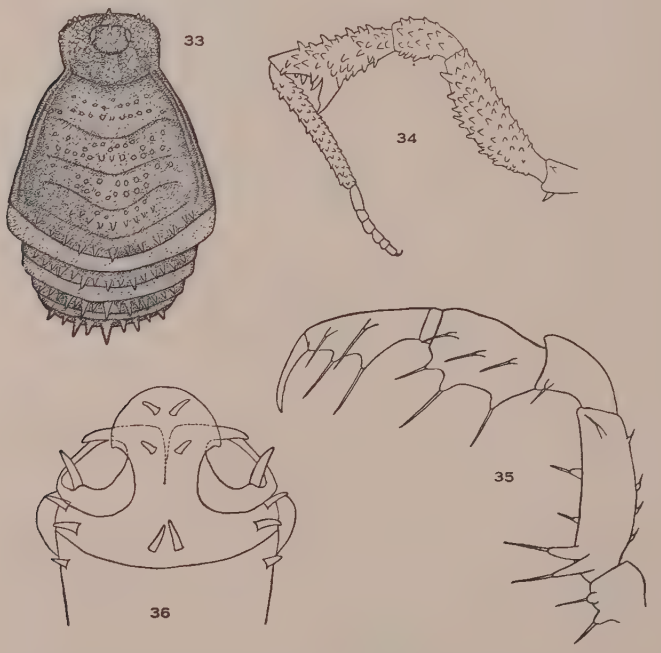
Body (*Fig. 33*): Eyemound separated from the anterior margin of the carapace by a distance equal to two-thirds of its length, with 2 tubercles on the median surface and a further tubercle between median line and the eyes. Carapace narrow, equal to five-ninths of widest portion of tergal region. There is a small spine on the median surface of anterior margin of the carapace and 3 small tubercles near the lateral margin. The scutal groove is curved. Four curved grooves separate the 5 tergal areas. All areas with small pustules, stronger on area 4. Posterior margin of scute and free tergites with spinous tubercles, stronger at the posterior

tergite. There are sharp tubercles around the margins of the anal plate and near the lateral margins of the sternites.

Genitalia are as shown in Figure 36.

Chelicerae: These are small and without tubercles.

Pedipalps are as shown in Figure 35. The structure of the pedipalp appears to differ little between species of this genus.



Figs. 33-36.—*Zalmoxis cardwellensis*, sp. nov.
Fig. 33, dorsal view of body of male (the free tergites are extended showing intersegmental membrane); Fig. 34, leg 4 of male; Fig. 35, prolateral surface of male pedipalp; Fig. 36, male genitalia.

Legs: All segments, except tarsi of legs 1-3, are granulate but without strong tubercles. The femur, patella and tibia of the 4th pair of legs are strongly developed and heavily spined (Fig. 34). Tibia not bent and armed with a strong spinous process on the ventral surface at about two-thirds of its length. The tarsal formula is 3-6-5,6. Distotarsi of legs 1 and 2 are 2 and 3 respectively.

Allotype Female

MEASUREMENTS (mm)

Scute: length 1.94, width 1.59

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.44	0.18	0.71	0.31	0.44	0.79	0.48	3.35
Leg 2	0.66	0.27	0.92	0.44	0.88	1.06	1.10	5.33
Leg 3	0.48	0.22	0.75	0.31	0.66	1.01	0.68	4.11
Leg 4	0.88	0.39	1.23	0.45	0.53	1.19	0.72	5.39
Pedipalp		0.15	0.53	0.27	0.35		0.27	1.57
			Chelicera: basal 0.32, second 0.62					0.94

Similar to male in appearance but tubercles and granules generally reduced in size. The femur, patella, and tibia of the 4th pair of legs are normal with a small spinous process on the ventral surface of the tibia. Tarsal formula as in male.

Types.—Holotype ♂. Cardwell Range, north Queensland, from leaf-mould (2.vi.1953, T. E. Woodward) ; allotype female, same data; paratypes, 2 ♀ ♀, same data; holotype and allotype (Q.M.) ; paratypes (A.M., C.M.).

Remarks.—This species is very closely related to *Z. darwinensis* Goodnight & Goodnight and should perhaps be given only subspecific rank. It is separated from *Z. darwinensis* by the presence of 6 segments to tarsus 2 instead of 5, by the presence of only 2 tubercles on the median surface of the eyemound instead of 4, and by the presence of 3 tubercles on each side of the anterior margin of the carapace.

Zalmoxis insula, sp. nov.

Figs. 37-39

Holotype Male

MEASUREMENTS (mm)

Scute: length 1.54, width 1.10

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.31	0.18	0.52	0.27	0.39	0.56	0.39	2.62
Leg 2	0.48	0.22	0.68	0.22	0.64	0.31	0.88	3.43
Leg 3	0.39	0.22	0.51	0.27	0.52	0.68	0.48	3.07
Leg 4	0.64	0.24	0.92	0.39	0.80	1.10	0.56	4.65
Pedipalp		0.18	0.44	0.21	0.22		0.18	1.23
			Chelicera: basal 0.35, second 0.60					0.95

Colour: Tergal region and free tergites uniform blackish brown. Carapace, chelicerae, pedipalps, and legs pale yellow with brown reticulate markings.

Body (*Fig. 37*) : Eyemound wider than long in ratio of 5 : 3 and separated from the anterior margin of the carapace by a distance equal to two-thirds its length. Slightly higher than wide, rounded, with 2 pairs of pustules. Anterior margin of the carapace with 3 sharp projections, 1 median and 1 at the outer surface of each chelicera, and 2-3 smaller tubercles near the outer margin. Scutal groove distinct, almost straight, tergal areas defined by four, slightly bowed, transverse grooves, of which

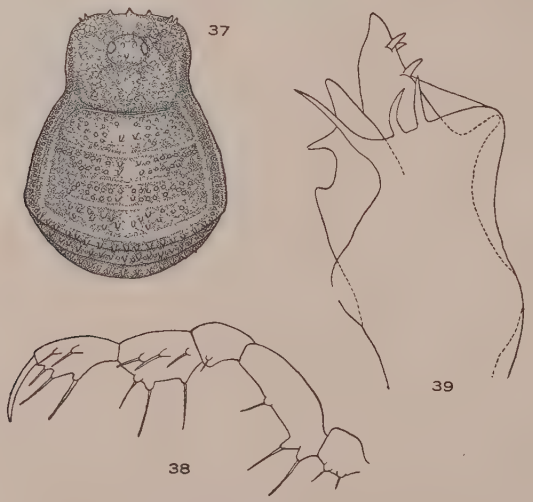
the 2nd and 3rd do not reach the lateral ridges. Carapace smooth but all tergal areas with small granules which are larger near the mid-surface. Posterior margin of scute and free tergites armed with small conical tubercles. Anal plate with a few small pustules. Genital operculum smooth, small.

Genitalia are as shown in Figure 39.

Chelicerae: Both segments smooth. The dorsal swelling of the basal segment extends over two-thirds of the segment.

Pedipalps (*Fig. 38*): All tubercles are provided with a long, apical seta. Trochanter with 2 small ventral tubercles. Femur with 2 strong tubercles on the proximoventral surface and a smaller mid-ventral tubercle. Tibia with 3 tubercles on both pro- and retroventral surfaces. Tarsus with 2 proventral and 3 retroventral tubercles.

Legs: All segments, except tarsi, closely granulate. Fourth leg not modified but with granulations on ventral surface of femur strong. Tarsal formula 3, 5, 5, 6. Distotarsi of legs 1 and 2 are 2 and 3 respectively.



Figs. 37-39.—*Zalmoxis insula*, sp. nov.
Fig. 37, dorsal view of body of male; Fig. 38, prolateral surface of male pedipalp; Fig. 39, lateral view of male genitalia.

Allotype Female

MEASUREMENTS (mm)
Scute: length 1.55, width 1.10

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.31	0.18	0.52	0.27	0.39	0.48	0.39	2.54
Leg 2	0.48	0.22	0.68	0.22	0.64	0.64	0.88	3.76
Leg 3	0.39	0.21	0.52	0.26	0.52	0.88	0.48	3.26
Leg 4	0.64	0.22	0.92	0.39	1.80	1.10	0.53	5.60
Pedipalp		0.17	0.44	0.22	0.21		0.18	1.22
Chelicera: basal 0.39, second 0.60								0.99

Similar to male in appearance. Tarsal formula 3, 5, 5, 6.

Types.—Holotype male, Dauan I., Torres Strait, north Queensland (6.v.1953, E. N. Marks); allotype female, same data; paratypes: numerous males and females, same data; holotype male; allotype female (Q.M.); paratypes (A.M., C.M., U.Q.).

Genus BOGANIA, gen. nov.

Carapace shorter than tergal region. Scute and eyemound granulate but without tubercles or spines. Tergal areas defined by almost straight transverse grooves. Eyemound removed from the anterior margin of the carapace by a distance equal to one-quarter its width. Legs unarmed. Tarsal formula 3, 5, 5, 6. Distotarsi of first 2 pairs of legs 2 and 3 respectively. Tarsi 3 and 4, with 2 smooth claws, without scopula. Sexual dimorphism shown in genital operculum.

Type species *Bogania granulata,* sp. nov.

This genus shows some affinity with *Zalmoxis* Soerensen but may be separated from it by the elongate genital operculum of the male, the incomplete segmentation of the tergal areas and the unusual structure of the penis.

BOGANIA GRANULATA, sp. nov.

Figs. 40-45

Holotype Male

MEASUREMENTS (mm)

Scute: length 1.85, width 1.80

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.52	0.27	0.92	0.39	0.68	0.76	0.52	4.06
Leg 2	0.72	0.22	1.10	0.44	1.32	1.15	1.06	6.01
Leg 3	0.48	0.26	0.92	0.39	0.80	1.10	0.72	4.67
Leg 4	0.64	0.24	1.32	0.48	1.19	1.49	0.92	6.08
Pedipalp		0.20	0.76	0.39	0.64		0.44	2.43
			Chelicera: basal 0.52, second 0.80					1.32

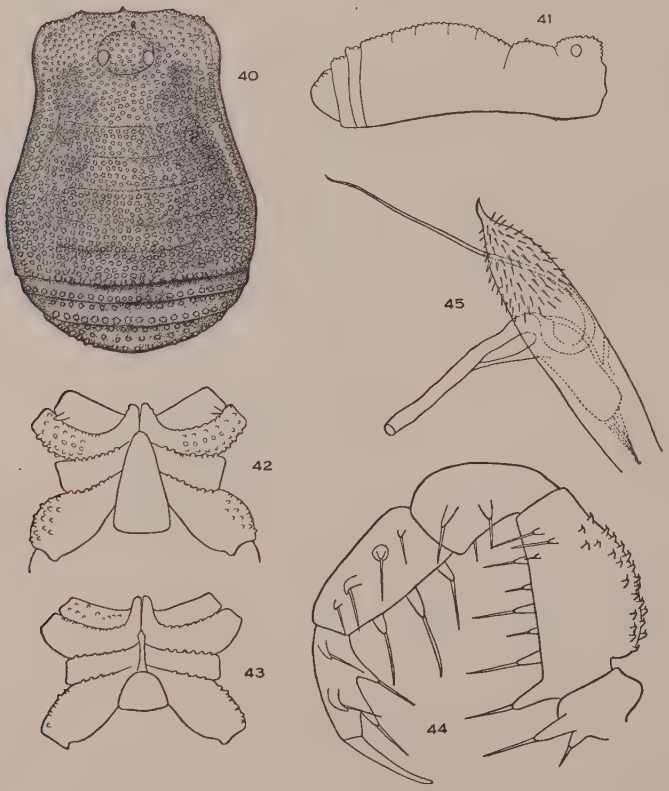
Colour: The entire animal is pale yellowish brown with slightly dark brown shading on the mid-lateral margins of the scute and on the sternites.

Body (*Figs. 40, 41*): The eyemound is granulate, squat, wider than long in the ratio of 5: 4, separated from the anterior margin of the carapace by a distance equal to one-quarter of its width. Scute and tergites closely granulate, without spines or tubercles. The scutal groove is distinct and the tergal areas are separated by transverse grooves which do not reach the lateral margins. The genital operculum is extremely large, subtriangular in shape, longer than it is wide at the base, in the ratio of 3: 2 and extends anteriorly to the 2nd pair of coxae (Fig. 42).

Genitalia (*Fig. 45*): Long and slender. Apical portion with numerous small setae and terminated with a sharp process. There are 2 elongate processes, 1 long and tubular and the other needle-like, which appear to be folded within the penis when it is retracted.

Chelicerae: There is a small lobe on the outer margin of the basal segment below the anterior margin of the carapace. The 2nd segment is armed with a number of small, sharp tubercles on the dorsal surface.

Pedipalps (*Fig. 44*): Trochanter with 2 strong conical tubercles on the ventral surface. Dorsal surface of femur rises sharply proximally, surface covered with small tubercles. There is a row of 6 conical tubercles



Figs. 40-45.—*Bogania granulata*, gen. et sp. nov.
Fig. 40, dorsal surface of body of male; Fig. 41, body of male from side; Fig. 42 anteroventral surface of body of male; Fig. 43, anteroventral surface of body of female; Fig. 44, prolateral surface of male pedipalp; Fig. 45, male genitalia.

along the ventral surface, proximal strongest, and 3 small tubercles on the distal prolateral surface. Patella with 2 pro- and 1 retrolateral tubercles. Tibia with 4 pro- and 3 retroventral tubercles. Tarsus with 2 tubercles on both pro- and retroventral margins.

Legs: These are very finely granulate and lack processes or tubercles. Tarsal formula 3, 5, 5, 6. Distotarsi of legs 1 and 2 are 2 and 3 respectively.

Allotype Female

MEASUREMENTS (mm)

Scute: length 1.55, width 1.55

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.52	0.18	0.88	0.31	0.60	0.68	0.52	3.69
Leg 2	0.72	0.22	1.28	0.27	1.10	1.10	1.32	6.01
Leg 3	0.48	0.18	0.87	0.30	0.68	0.92	0.51	3.94
Leg 4	0.68	0.31	1.10	0.44	0.97	1.36	0.82	5.68
Pedipalp		0.18	0.64	0.28	0.48		0.44	2.02
			Chelicera: basal 0.44, second 0.60					1.04

Differing from male as follows: no lateral lobe present on the basal segment of the chelicera. Genital operculum normal, as wide as it is long (Fig. 43). Tarsal formula 3, 5, 5, 6. Pedipalp smaller but essentially similar in structure.

Types.—Holotype male and allotype female, Bogan River, N.S.W. (Aug. 1952, J. W. T. Armstrong); paratypes, numerous specimens with the same data as holotype; holotype male, allotype female (A.M.); paratypes (Q.M., C.M., N.M., U.Q.).

Subfamily **IBALONIINAE** Roewer

Genus AUSTRIBALONIUS, gen. nov.

Anterior margin of the carapace with an elongated lobe on each lateral corner. Eyes widely separated with 3 spines on median surface and a strong spine directed over the anterior margin of the carapace from in front of each eye. Tergal areas not defined. Tergal region with 3 pairs of spinous tubercles. Pedipalp slightly longer than the scute. Leg 1 strongly spined. Tarsal formula 3, 2, 4, 4. Distotarsi of legs 1 and 2 are 2 and 1 respectively. Scopula absent.

Type species *Austribalonius horridus*, sp. nov.

Closely related to *Metibalonius* Roewer, which is known only from New Guinea. It may be separated from it by the more moderate development of the median ocular spines and the presence of 4 segments for the 3rd and 4th tarsi instead of 5 as in *Metibalonius*. The species described below is the first record of the subfamily Ibaloniinae from Australia.

AUSTRIBALONIUS HORRIDUS, sp. nov.

Figs. 46-48

Holotype Female

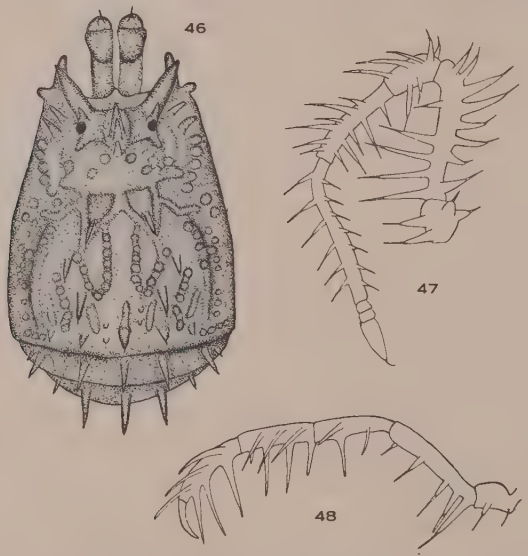
MEASUREMENTS (mm)

Scute: length 1.59, width 1.41

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.27	0.22	0.68	0.31	0.44	0.68	0.31	2.91
Leg 2	0.44	0.22	1.79	0.35	1.76	1.36	0.52	3.44
Leg 3	0.52	0.27	1.28	0.30	0.97	1.24	0.27	2.85
Leg 4	0.68	0.23	1.59	0.36	1.32	1.81	0.28	6.27
Pedipalp		0.18	0.56	0.44	0.44		0.44	2.06
			Chelicera: basal 0.31, second 0.52					0.83

Colour: Pale yellowish brown with dark shading on the mid-lateral surfaces of the scute. Chelicerae and pedipalps with black reticulate markings. Legs with dark shading.

Body (*Fig. 46*) : Distance between the eyes is equal to one-third the width of the carapace in that region. There is a short spinous projection immediately in front of the eyes, below which there is a further strong spinous process projecting forward over the anterior margin of the carapace. The median surface between the eyes is raised and armed with a row of 3 erect spines, stronger anteriorly. Each anterior corner of the



Figs. 46-48.—*Austribalonius horridus*, gen. et sp. nov.
Fig. 46, dorsal surface of body; Fig. 47, first leg;
Fig. 48, prolateral view of pedipalp.

carapace with a strong anteriorly directed process which is provided with a small accessory lobe or tubercle on the outer margin. There are 2 elongate tubercles behind the lateral margins of the carapace. Scutal groove distinct. Dorsal pattern indistinct, formed by ridges and separate pustules as shown in Figure 46. There are 3 pairs of elongate tubercles on the tergal region which appear to indicate areas 1-3. Tergal areas are not defined by transverse grooves. Posterior margin of scute with few relatively small conical tubercles. Free tergites 1 and 2 with a transverse row of strong spinous tubercles, tergite 3 with small rounded tubercles. Anal plate and genital operculum with a few pustules.

Chelicerae: Basal segment smooth. Second segment with 2-3 small, dorsally situated, tubercles. Fingers strongly developed, almost equal in length to rest of segment.

Pedipalps: Slender, slightly longer than body and strongly spined as shown in Figure 48.

Legs: First leg strongly spined (Fig. 47). The femora of the remaining legs are armed with few elongate tubercles which are much smaller than on the 1st femur. Tarsal formula 3, 2, 4, 4. Distotarsi of legs 1 and 2 are 2 and 1 respectively.

Type.—Holotype female, Cardwell Range, south side (2.vi.1953, T. E. Woodward) (Q.M.).

Family **TRIAENONYCHIDAE** Soerensen
Subfamily **TRIAENONYCHINAE** Pocock
Tribe TRIANENONYCHINI Forster
Genus NUNCIELLA Roewer 1928

NUNCIELLA MONTANA, sp. nov.

Figs. 49-51

Holotype Male

MEASUREMENTS (mm)

Scute: length 3.08, width 3.01

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.88	0.35	1.19	0.52	0.97	1.15	0.72	5.78
Leg 2	1.06	0.44	1.64	0.68	1.32	1.55	1.59	8.28
Leg 3	1.04	0.31	1.06	0.60	0.92	1.14	0.56	5.63
Leg 4	1.32	0.44	1.49	0.72	1.32	1.70	1.01	8.00
Pedipalp		0.32	1.45	0.52	1.06		0.48	3.83
			Chelicera: basal 1.19, second 1.59					2.78

Colour: Ground colour pale yellow with black shading on the scute forming 3 lateral and 1 postero-median patch. Free tergites and the sternites heavily shaded. Appendages with dark reticulate markings.

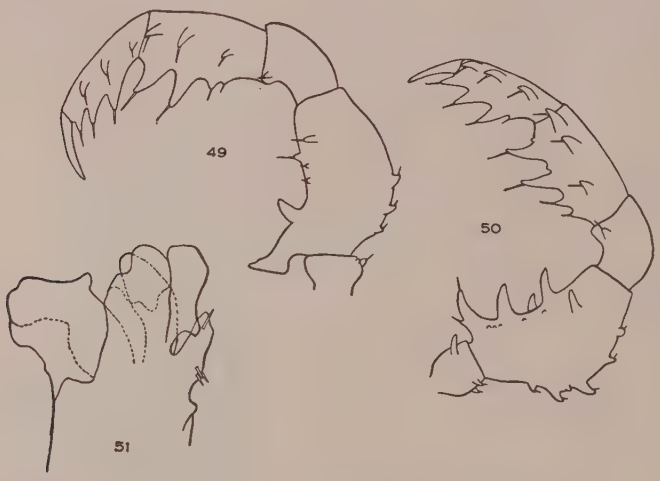
Body: The eyemound is low, evenly rounded, rising directly from the anterior margin of the carapace. Scute low, smooth. Scutal groove faintly visible on the median surface of the scute. Tergal region without transverse grooves. There is a row of small granules on the posterior margin of the scute and the free tergites. Genital operculum, sternites, and anal plate smooth.

Genitalia: Complex, as shown in Figure 51.

Chelicerae: Typical, with a strong process on the outer proximodorsal surface of the basal segment.

Pedipalps (*Fig. 49*): Femur with a strong clavate tubercle on the proximoventral surface, directed back, with a small, sharp, anteriorly directed tubercle near the base. There is a further small spinous tubercle on the ventral surface at about two-thirds and a similar tubercle on the prolateral surface at this distance. Dorsal surface with 3 sharp tubercles on the proximal half. Patella with a small distal prolateral tubercle. Tubercles on tibia and tarsus strong, spinous, 3 on both ventral margins but 1st retroventral of tibia relatively small.

Legs: Coxa 1 with the usual strong clavate tubercle on the distoventral surface. There is a strong, sharp tubercle on the retrolateral surface of coxa 2 and the prolateral surface of coxa 4. The legs are finely granulate and lack tubercles. Tarsal formula 3, 7-8, 4, 4. Distotarsi of legs 1 and 2 are 2 and 4 respectively.



Figs. 49-51.—*Nunciella montana*, sp. nov.
Fig. 49, prolateral surface of male pedipalp; Fig. 50, prolateral surface of female pedipalp; Fig. 51, lateral view of male genitalia.

Allotype Female

MEASUREMENTS (mm)

Scute: length 3.12, width 3.12

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.88	0.31	1.32	0.60	0.88	1.10	0.68	5.77
Leg 2	1.32	0.44	1.76	0.68	1.36	1.64	1.59	8.79
Leg 3	1.10	0.35	1.01	0.56	0.92	1.28	0.88	6.10
Leg 4	1.55	0.44	1.70	0.88	1.32	1.98	1.15	9.02
Pedipalp		0.39	1.32	0.67	1.10		0.88	4.36
			Chelicera: basal 1.01, second 1.32					2.33

The scute is more heavily shaded than in the male, forming a chevron pattern. Chelicerae are smaller and lack a process on the basal segment. Pedipalps are as shown in Figure 50. The proximoventral tubercle of the femur is in the form of an unevenly bifid tubercle and there are 2 relatively strong spinous tubercles on the ventral surface near the midpoint. Tarsal formula 3, 9-11, 4, 4.

Types.—Holotype male, allotype female, paratype 1 female, Rock Creek, Mt. Kosciusko, 5550 ft, New South Wales (25.xi.1952, A. Musgrave), among snowgrass against rocks (A.M.).

Remarks.—*N. montana* may be separated from all other species of this genus by the absence of strong tubercles from the mid-ventral surface of the pedipalp femur, the small size of the tubercles on the ventral margins of tibia, and the presence of tubercles on the ventral surfaces of the femora of legs 3 and 4.

NUNCIELLA WOOLCOCKI, sp. nov.

Figs. 52-56

Holotype Male

MEASUREMENTS (mm)

Scute: length 3.52, width 3.08

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.68	0.31	1.32	0.68	1.10	1.15	0.88	6.12
Leg 2	1.32	0.44	1.85	0.88	1.55	1.76	1.59	9.39
Leg 3	1.15	0.44	1.01	0.64	0.92	1.41	0.88	6.45
Leg 4	1.36	0.52	1.76	0.80	1.59	2.20	1.10	9.33
Pedipalp		0.43	1.78	1.06	1.76		1.15	6.18
Chelicera: basal 1.32, second 1.24								2.56

Colour: Scute and free tergites dull brown with an indistinct pattern on the scute. Appendages yellowish brown.

Body: The eyemound is low, twice as wide as it is high, smooth, evenly rounded, rising from the anterior margin of the carapace (Fig. 52). The scute is dull but does not appear to be granulate. Scutal groove only faintly visible on the median surface. Tergal region without any trace of segmentation. Free tergites smooth. Anal plate, sternites, and genital operculum smooth.

Genitalia: Complex, appearing in lateral view as shown in Figure 56.

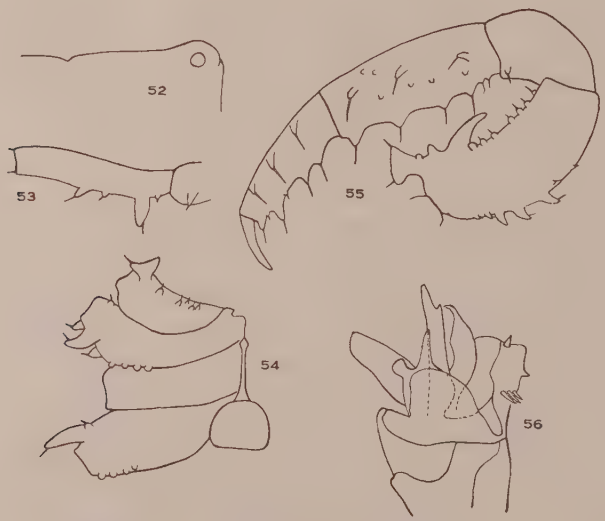
Chelicerae: Basal segment with a strong but elongate lobe on the outer proximodorsal surface and a few small pustules on the mid-dorsal surface. Second segment with a few small sharp tubercles along the dorsal surface.

Pedipalps (*Fig. 55*) : There is a strong tubercle on the proximoventral surface, directed back, with the distal portion broadly clavate. There is an equally strong but sharp tubercle on the anterior surface which is curved forward. There are 6 or 7 small rounded tubercles lining the proventral margin. Dorsal surface with 3 strongly sharp tubercles. The tubercles on the tibia are small, 4 retroventral, 3 proventral. Tarsus with 3 tubercles on both ventral margins.

Legs (*Figs. 53, 54*) : Coxa 1 with a strong bifid tubercle on the distoventral surface, which rests against the clavate tubercle on the proximoventral surface of the pedipalp femur. There is a strong spinous tubercle on the retrolateral surface of coxa 2 and the prolateral surface of coxa 4. Femur 3 is armed with a strong spinous tubercle near the proximoventral surface and 2 further smaller tubercles near the mid-ventral surface. There are also 3 small spinous tubercles on the ventral surface of the femur of leg 4. Tarsal formula 3, 9, 4, 4. Distotarsi of legs 1 and 2 are 2 and 3 respectively.

Type.—Holotype male, Ginnini Flats, A.C.T., 5700 ft, in *Sphagnum* moss (10.xi.1949, L. Woolcock) (A.M.).

Remarks.—*N. woolcocki* may be separated from all other species of *Nunciella* by the absence of strong tubercles from the mid-ventral surface of the pedipalp femur, the small size of the tubercles on the ventral margins of the tibia, and the presence of tubercles on the ventral surfaces of the femora of legs 3 and 4.



Figs. 52-56.—*Nunciella woolcocki*, sp. nov.
Fig. 52, lateral view of eyemound; Fig. 53, trochanter and femur of leg 3; Fig. 54, coxae, sternum and genital operculum of male; Fig. 55, prolateral surface of male pedipalp; Fig. 56, lateral view of male genitalia.

Genus CLUNIELLA, gen. nov.

Small, carapace equal in length to, or longer than tergal region. Eyemound unarmed, more or less rounded, rising directly from the anterior margin of the carapace. Scutal groove shallow. Tergal areas not defined by transverse grooves. Scute and free tergites unarmed. Calcaneus of legs 1-4 usually much shorter than, but sometimes almost equal in length to the astragalus. Astragalus not notched. Tarsal formula 3, 4-6, 4, 4. Distotarsi of legs 1 and 2 are 2 and 3 respectively. Median prong of tarsal claws 3 and 4 much stronger than lateral branches. Sexual dimorphism sometimes present in shape of genital operculum. Process never present on basal segment of chelicera.

Type species *Cluniella minuta*, sp. nov.

This genus is similar in general appearance to *Nunciella* Roewer, but the species described below are much smaller in size and have fewer segments to tarsus 2. The number of these segments is relatively variable within *Nunciella* spp., but stable within the known *Cluniella* spp., as is often the case in triaenonychids where the number is reduced to 6 or less. There is a superficial resemblance with the New Zealand *Nuncia* spp. which are found living in a similar habitat, namely leafmould accumulations in forested areas, but the structure of the male genitalia indicates parallel development rather than close affinity. The structure of the male genitalia of the three species described below suggests that when the Australian leafmould fauna is better known it may be found that the species grouped below are not truly congeneric.

Cluniella minuta, sp. nov.

Figs. 57-60

Holotype Male

MEASUREMENTS (mm)

Scute: length 1.75, width 1.36

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.49	0.24	0.63	0.37	0.57	0.62	0.63	3.55
Leg 2	0.73	0.27	0.90	0.49	0.87	0.91	1.22	5.39
Leg 3	0.65	0.25	0.65	0.37	0.55	0.61	0.65	3.73
Leg 4	0.74	0.27	0.99	0.39	0.77	0.90	0.99	5.05
Pedipalp		0.24	0.55	0.42	0.40		0.45	2.06
			Chelicera: basal 0.49, second 0.72					1.21

Colour: Ground colour of body pale yellowish brown but heavily shaded with blackish brown. Chelicerae and pedipalps with reticulate black markings. Legs dark.

Body: The eyemound is smooth, rising steeply up from the anterior margin of the carapace but gently rounded posteriorly (Fig. 57). Scute finely granulate without pustules or tubercles. Scutal groove shallow, tergal areas not defined. Posterior margin of scute and free tergites without pustules or tubercles. Sternum narrow, genital operculum smooth.

Genitalia: Long and extremely slender and bent distally. The distal portion is simple and is shown in Figure 60.

Chelicera: Basal segment smooth, 2nd segment with 2 low tubercles on dorsal surface.

Pedipalps (*Fig. 58*) : Trochanter with 2 small tubercles on both dorsal and ventral surfaces. Femur with a strong unevenly bifid tubercle on the proximoventral surface and 3 smaller simple tubercles along the ventral surface. Dorsal surface with 3 sharp tubercles.

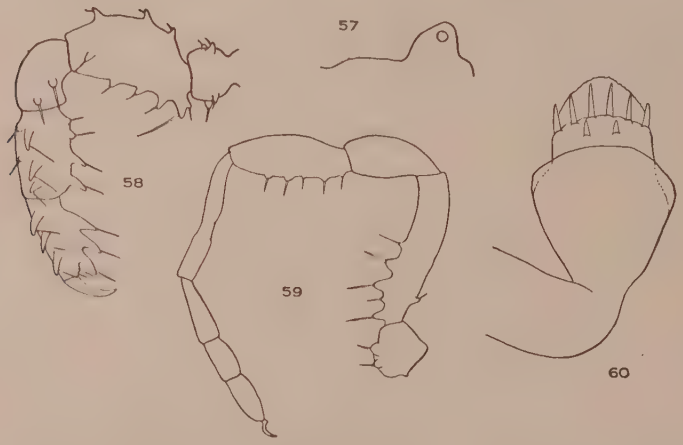
Legs: Trochanter, femur, and tibia of leg 1 with ventral tubercles (Fig. 59). Legs otherwise finely granulate. Retrolateral surface of coxa 2 and prolateral surface of coxa 4 with a small tubercle. Tarsal formula 3, 6, 4, 4. Distotarsi of legs 1 and 2 are 2 and 3 respectively.

Allotype Female

MEASUREMENTS (mm)

Scute: length 1.64, width 1.77

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.49	0.25	0.75	0.37	0.55	0.67	0.72	3.80
Leg 2	0.74	0.24	0.99	0.42	0.84	0.84	1.30	5.37
Leg 3	0.62	0.24	0.69	0.30	0.63	0.75	0.75	3.98
Leg 4	0.75	0.29	0.99	0.42	0.85	1.03	1.07	5.40
Pedipalp		0.35	0.65	0.45	0.40		0.42	2.27
			Chelicera: basal 0.49, second 0.67					1.16



Figs. 57-60.—*Cluniella minuta*, gen. et sp. nov.
Fig. 57, lateral view of eyemound; Fig. 58, prolateral surface of male pedipalp; Fig. 59, leg 1 of male; Fig. 60, male genitalia.

Similar to male in structure.

Types.—Holotype male, allotype female, and paratypes, 1 ♂, 3 ♀♀, Mt. Clunie, east spur, south Queensland, from leafmould ex rain-forest, (5.iv.1953, T. E. Woodward); holotype male, allotype female (Q.M.), paratypes (A.M., C.M., U.Q.).

CLUNIELLA DISTINCTA, sp. nov.

Figs. 61-65

Holotype Male

MEASUREMENTS (mm)

Scute: length 1.25, width 1.15

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.31	0.15	0.45	0.26	0.41	0.51	0.45	2.54
Leg 2	0.45	0.19	0.66	0.36	0.61	0.61	0.82	3.70
Leg 3	0.31	0.20	0.51	0.26	0.36	0.45	0.45	2.54
Leg 4	0.56	0.21	0.61	0.31	0.56	0.71	0.66	3.62
Pedipalp		0.20	0.56	0.30	0.41		0.31	1.78
			Chelicera: basal 0.31, second 0.56					0.87

Colour: Ground colour of body orange-brown, with a black patch on the mid-lateral surfaces of the scute, and black reticulate markings on the carapace. Dorsal surfaces of chelicerae and pedipalps with black reticulate markings. Legs banded with alternate pale cream and brown bands.

Body: The eyemound rises steeply up from the anterior margin of the carapace but slopes gently back to the posterior margin (Fig. 61). The carapace is twice as long as the tergal region. There are 2 small tubercles on the anterior margin of the carapace, 1 on each mid-lateral surface. Scute and free tergites smooth. There appears to be no segmentation in the tergal region. The genital operculum is elongate (Fig. 64) twice as long as it is wide at the base, extending to the posterior margin of the 2nd pair of pedal coxae.

Genitalia (*Fig. 65*): Slender with T-shaped apical extension. There is a pair of thin plates immediately behind the apical extension and 2 further pairs of processes more posterior, of which the anterior are strong and spinous and the posterior lobular.

Chelicerae: Basal segment with a sharp distodorsal tubercle. Second segment with 2-3 small rounded dorsal tubercles.

Pedipalps (*Fig. 62*): Trochanter with a strong ventral tubercle. Femur with a strong, unevenly bifid tubercle on the proximoventral surface which is directed back and 2 further simple tubercles of which the proventral is the smaller. There are 2 small tubercles near the mid-ventral surface and a similar prolateral tubercle. Dorsal surface with 3 relatively strong, sharp tubercles. Patella with 2 small prolateral tubercles. Tibia and tarsus with 3 strong tubercles on both pro- and retroventral margins.

Legs: Retrolateral surface of coxa 2 and prolateral surface of coxa 4 with a strong, spinous tubercle. Legs with few granules, stronger on the ventral surface of the tibia and femur of leg 1. Tarsal formula 3, 4, 4, 4. Distotarsi of legs 1 and 2 are 2 and 3 respectively.

Allotype Female

MEASUREMENTS (mm)

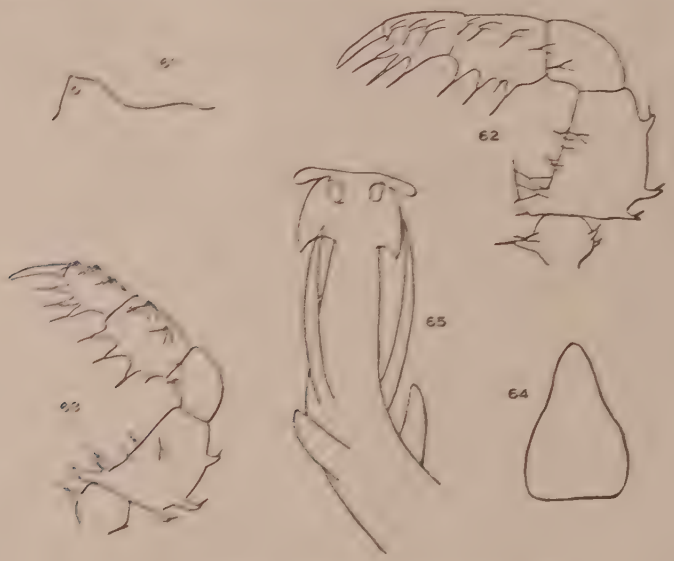
Scute: length 1.15, width 1.10

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.41	0.15	0.45	0.26	0.36	0.41	0.45	2.49
Leg 2	0.61	0.20	0.71	0.25	0.56	0.56	0.77	3.66
Leg 3	0.41	0.15	0.51	0.26	0.41	0.42	0.51	2.67
Leg 4	0.51	0.21	0.71	0.31	0.51	0.71	0.61	3.57
Pedipalp		0.20	0.51	0.21	0.36		0.26	1.54
			Chelicera: basal 0.31, second 0.56					0.87

Differing from male in the shape of the genital operculum, which is normal in appearance, being slightly wider than it is long. The sternum is broadly triangular and the pedipalps are as shown in Figure 63.

Types.—QUEENSLAND: Mt. Hobwee, Lamington Plateau, ex leafmould from rain-forest (27.viii.1953, T. E. Woodward), holotype ♂, allotype ♀,

2 ♂♂, 2 ♀♀, paratypes; Binna Burra (29.vii.1952, T. E. Woodward), 2 ♂♂, 1 ♀ paratypes; Mt. Ballow, ex leafmould (4.iv.1953, T. E. Woodward), 1 ♀ paratype. Holotype ♂, allotype ♀ (Q.M.), paratypes (A.M., C.M., U.Q.).



Figs. 61-65.—*Cluniella distincta*, sp. nov.
Fig. 61, lateral view of eyemound; Fig. 62, prolateral surface of male pedipalp; Fig. 63, prolateral surface of female pedipalp; Fig. 64, male genital operculum; Fig. 65, male genitalia.

Remarks.—Separated from both *ornata* and *minuta* by the elongate genital operculum of the male and the distinctive structure of the male genitalia.

Cluniella ornata, sp. nov.

Figs. 66-70

Holotype Male

MEASUREMENTS (mm)

Scute: length 1.48, width 1.43

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.40	0.22	0.65	0.27	0.47	0.52	0.62	3.15
Leg 2	0.59	0.22	0.83	0.42	0.89	0.89	0.86	4.70
Leg 3	0.56	0.20	0.60	0.37	0.65	0.67	0.49	3.54
Leg 4	0.62	0.25	0.92	0.40	0.80	0.98	0.68	4.65
Pedipalp		0.15	0.47	0.31	0.37		0.35	1.65
			Chelicera: basal 0.37, second 0.57					0.94

Colour: Ground colour of body orange-brown but shaded with dark brown. Dorsal surfaces of chelicerae and pedipalps with dark reticulate markings. Legs blackish.

Body (*Fig. 66*) : The eyemound rises directly from the anterior margin of the carapace. It is round in outline when seen from above, but higher than it is wide, smooth apically with few small pustules. Anterior margin of the carapace without spines but with a row of contiguous pustules which extend back down the lateral margin of the carapace to the level of the scutal groove. Scutal groove shallow. Tergal areas not defined by transverse grooves. Areas 1-4 each with a small median pair of tubercles. Posterior margin of scute and free tergites smooth.

Genitalia are as shown in Figure 70. The aedeagus is long and tubular and provided with small setae distally. It is supported by an elongated and bifurcate process.

Chelicerae are smooth.

Pedipalps (*Fig. 69*) : Femur with 2 strong tubercles near the proximo-ventral surface and 1 smaller mid-ventral tubercle. There are 3 small tubercles on the promixal half of the dorsal surface and 3 further tubercles on the distodorsal and prolateral surfaces. Tibia with 3 tubercles on both ventral margins. Tarsus with 2 proventral and 3 retroventral tubercles.

Legs: There is a strong lobe on the retrolateral surface of coxa 2 and the prolateral surface of coxa 4. Tarsal formula 3, 4, 4, 4. Distotarsi of legs 1 and 2 are 2 and 3 respectively. There are tubercles on the ventral surfaces of the trochanter, femur, and tibia of the 1st pair of legs (Fig. 68). Legs otherwise smooth.

Allotype Female

MEASUREMENTS (mm)

Scute: length 1.72, width 1.65

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.49	0.22	0.75	0.37	0.50	0.62	0.63	3.58
Leg 2	0.67	0.21	0.85	0.40	0.89	0.92	1.01	4.95
Leg 3	0.62	0.25	0.73	0.37	0.62	0.80	0.65	4.04
Leg 4	0.75	0.30	0.97	0.47	0.90	0.89	0.75	5.03
Pedipalp		0.22	0.48	0.29	0.42		0.32	1.73
Chelicera: basal 0.49, second 0.72								1.21

Similar in appearance to male.

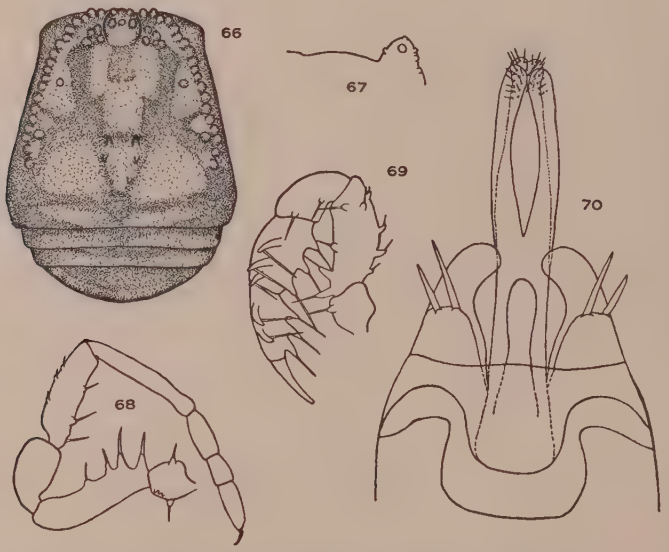
Types.—QUEENSLAND: Mt. Tambourine, near Curtis Falls, ex leaf-mould from rain-forest (8.v.1953, T. E. Woodward), holotype male, allotype female and numerous paratypes; Binna Burra, Lamington Plateau, ex leafmould from rain-forest (28.vii.1953, T. E. Woodward), numerous paratypes. Holotype male, allotype female (Q.M.), paratypes (C.M., A.M., U.Q.).

Remarks.—This distinctive species may be readily recognized by the row of pustules along the anterior and lateral margins of the scute.

Genus HOLONUNCIA, gen. nov.

Carapace shorter than scute. Eyemound rounded, unarmed, rising from immediately behind the anterior margin of the carapace. Small

tubercles present behind the anterior margin of the carapace. Tergal areas not defined by grooves but with transverse rows of granules. Free tergites with similar rows of granules. Calcaneus of legs shorter than astragalus. Tarsal formula 4, 13-16, 4, 4. Distotarsi of legs 1 and 2 are 2 and 4 respectively. Median prong of claws 3 and 4 much stronger than lateral branches.



Figs. 66-70.—*Cluniella ornata*, sp. nov.
Fig. 66, dorsal surface of body of male; Fig. 67, lateral view of eyemound; Fig. 68, leg 1 of male; Fig. 69, prolateral surface of male pedipalp; Fig. 70, male genitalia.

Type species *Holonuncia cavernicola*, sp. nov.

Although somewhat similar to *Nunciella* in external appearance the structure of the male genitalia suggests that this genus is more closely related to *Jenolanicus* and *Heteronuncia* from which it is immediately distinguished by the lack of ocular and scutal spines. The presence of tubercles behind the anterior margin of the carapace, the absence of a knob on the basal segment of the chelicera of the male, the structure of the proximoventral tubercle of the pedipalp femur and the different form of the male genitalia separates *Holonuncia* from *Nunciella*, while the absence of spinous tubercles from the tergal region separates it from *Paranuncia* Roewer. *Neonuncia tuberculata* Roewer, 1914 must also be placed in *Holonuncia*. *Neonuncia* Roewer, 1914 is now restricted to a group of species found in New Zealand and the Auckland and Campbell Is. (Forster 1954) which are closely related to *Nunciella* Roewer.

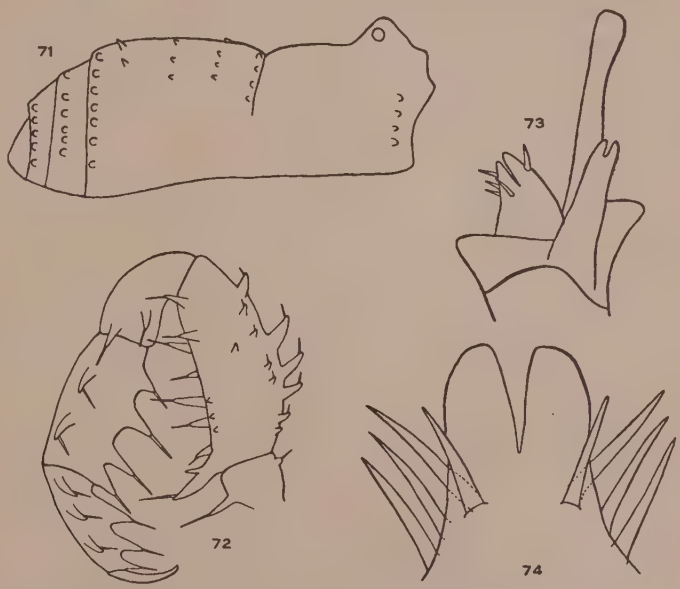
HOLONUNCIA CAVERNICOLA, sp. nov.
Figs. 71-74

Holotype Male

MEASUREMENTS (mm)

Scute: length 2.68, width 2.68

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.88	0.44	2.51	0.88	2.24	3.08	1.32	11.35
Leg 2	1.10	0.48	4.18	1.32	3.99	4.85	4.93	20.85
Leg 3	1.19	0.48	3.08	0.97	2.42	3.96	1.94	14.04
Leg 4	1.76	0.64	4.40	1.10	2.86	5.92	2.73	19.41
Pedipalp		0.48	2.20	0.80	1.24		1.32	6.04
Chelicera: basal 1.15, second 1.81								2.96



Figs. 71-74.—*Holonuncia cavernicola*, gen. et sp. nov. Fig. 71, lateral view of body of male; Fig. 72, prolateral view of male pedipalp; Fig. 73, male genitalia; Fig. 74, ventral plate of male genitalia.

Colour: All specimens are uniform pale yellowish brown.

Body (*Fig. 71*) : Eyemound is evenly conical and smooth, wider than it is long in the ratio of 7 : 5, and separated from the anterior margin of the carapace by a distance equal to four-fifths of the length of the eyemound. There are 3-4 small tubercles behind the anterior margin of the carapace near the lateral margins. Carapace otherwise smooth. Scutal groove shallow, restricted to the median surface. Tergal region without groove, smooth apart from 5 rows of granules. Free tergites each with a

transverse row of granules. Sternum narrow. Genital operculum smooth, as long as wide.

Genitalia (*Figs. 73, 74*): The aedeagus is simple, rod-like. Ventral plate with 2 groups of strong setae each consisting of 1 superior and 3 inferior. Dorsal plate single with a short antero-median notch.

Chelicerae: Relatively large. There are 2 small tubercles on the mid-dorsal surface of the basal segment and a stronger tubercle on the distodorsal surface. Second segment with 5-6 sharp tubercles on the dorsal surface.

Pedipalps (*Fig. 72*): Relatively slender. Trochanter with a strong ventral and small dorsal tubercle. Femur with 6 elongate tubercles along the ventral surface of which the proximal is strongest and is provided with a slender accessory spine at half of its length. There are 2 further tubercles on the distoventral prolateral surface and 5-6 tubercles on the dorsal surface. Patella with 2 prolateral tubercles. Tibia with 2 spinous tubercles on the proventral and 4 on the retroventral margins. Tarsus with 3 tubercles on both ventral margins.

Legs: There are 4 elongate tubercles along the proventral margin of the 1st coxae and 2 sharp tubercles on the retrolateral surface of coxa 2 and the prolateral margin of coxa 4. Legs otherwise without tubercles. Tarsal formula 4, 14-16, 4, 4. Distotarsi of legs 1 and 2 are 2 and 4 respectively. Calcaneus of 1st leg weakly notched.

Types.—Holotype male, Jenolan Caves, N.S.W. (A.M. No. K13022). Paratypes: 1 ♂, same data (A.M. K12570); 1 ♂, Yarrangobilly Caves, N.S.W. (coll. Stead, A.M. No. K41797).

Remarks.—Separated from *H. tuberculata* Roewer by the different disposition of the tubercles on the pedipalp and the fewer number of tubercles behind the anterior margin of the carapace.

Genus LOMANELLA Pocock 1903

LOMANELLA PARVA, sp. nov.

Figs. 75-78

Holotype Male

MEASUREMENTS (mm)

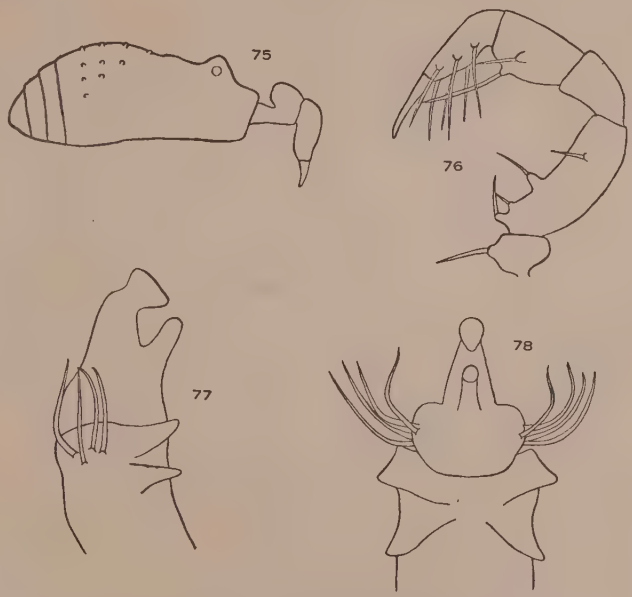
Scute: length 1.0, width 0.77

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.31	0.10	0.45	0.21	0.29	0.26	0.31	1.93
Leg 2	0.32	0.09	0.45	0.26	0.45	0.36	0.45	2.38
Leg 3	0.26	0.10	0.41	0.20	0.36	0.36	0.31	2.00
Leg 4	0.36	0.12	0.51	0.27	0.46	0.51	0.36	2.59
Pedipalp		0.08	0.45	0.16	0.20		0.26	1.15
Chelicera: basal 0.21, second 0.41								0.62

Colour: Entire animal pale yellowish brown but with faint black shading on the scute.

Body (*Fig. 75*): The eyemound is evenly rounded and smooth, separated from the anterior margin of the carapace by a distance which is slightly less than the length of the eyemound. Scute finely and evenly granulate, anterior margin smooth. Scutal groove faintly visible on median surface. Tergal areas not defined but tergal region with 4 transverse rows of small granules. Free tergites and sternites without tubercles or pustules. Sternum narrow. Genital operculum smooth.

Genitalia (*Figs. 77, 78*): Aedeagus with 2 apical processes, 2 groups of 4 long setae.



Figs. 75-78.—*Lomanella parva*, sp. nov.
Fig. 75, lateral view of body and chelicera of male; Fig. 76, prolateral surface of male pedipalp; Fig. 77, lateral view of male genitalia; Fig. 78, ventral view of male genitalia.

Chelicerae: Both segments are smooth. Basal segment strongly distended on the distodorsal surface.

Pedipalps (*Fig. 76*): The tubercles are small but are provided with strong setae. There is a single tubercle on the ventral surface of the trochanter and 3 on the proximoventral surface of the femur, of which the median is smaller. There is a small tubercle on the prolateral surface of the femur at about two-thirds of its length. Tibia with 2 tubercles, 1 proventral and the other retroventral. Tarsus with 3 tubercles on both ventral margins.

Legs: Finely granulate. Tarsal formula 2, 2, 3, 3.

Allotype Female

MEASUREMENTS (mm)

Scute: length 1.05, width 0.82

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.26	0.09	0.41	0.18	0.29	0.26	0.31	1.80
Leg 2	0.41	0.09	0.41	0.26	0.38	0.36	0.46	2.37
Leg 3	0.31	0.09	0.36	0.17	0.36	0.36	0.32	1.97
Leg 4	0.41	0.11	0.45	0.26	0.41	0.45	0.36	2.45
Pedipalp		0.05	0.40	0.13	0.16		0.20	0.94

Chelicera: basal 0.21, second 0.42 0.63

Pedipalp: More slender. Tarsal formula 3, 3, 4, 4.

Types.—Holotype ♂ and allotype ♀, Wallaby Beach, Port Davey, south-west Tasmania, ex leafmould (29.i.1954, E. N. Marks) (Q.M.).

Remarks.—Three species have been previously recorded. *L. raniceps* Hogg and *L. atrolutea* Roewer from Tasmania and *L. kallista* Forster from Victoria. The present species is much smaller than any of these species and may be separated from them by the presence of 3 tubercles on the proximoventral surface of the femur of the pedipalp instead of the single tubercle found in all other species, and also by the different tarsal count which is 3, 5, 4, 4 in these species. The difference shown between the tarsal formula of the male and female specimens described above is interesting, indicating the division of the distal segment in the female. Future collecting will determine whether this is a fixed dimorphic character of the species described or merely variation.

Genus JENOLANICUS Roewer 1914

JENOLANICUS TAMBOURINEUS Roewer

Figs. 79-81

Jenolanicus tambourineus Roewer, 1920, Ark. Zool. Stockholm 13: 5.
Jenolanicus tambourineus Roewer, 1923, Die Weberknechte der Erde, Jena, 599.

Holotype Female

MEASUREMENTS (mm)

Scute: length 3.08, width 3.17

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.79	0.44	1.76	0.88	1.54	1.98	0.88	8.27
Leg 2	1.41	0.53	2.73	1.10	2.64	3.30	2.42	14.13
Leg 3	1.32	0.57	2.91	0.88	1.76	2.51	1.41	11.36
Leg 4	1.54	0.62	2.92	0.97	2.20	3.91	1.36	13.52
Pedipalp		0.48	1.68	0.96	1.28		0.92	5.32

Chelicera: basal 0.71, second 1.32 2.03

Colour: Entire animal pale yellowish brown, but this is probably due to fading as Roewer records legs and body dull brown.

Body: The eyemound is separated from the anterior margin of the carapace by a distance equal to one-quarter of its width, with strong, straight apical spine, which is equal in height to the eyemound proper and is directed slightly forward. There are 4 small spines on the anterior

margin of the carapace, the inner pair are level with the lateral margins of the eyemound, while the outer 2 are situated almost halfway between the former 2 and the lateral margins. There is a much stronger spine behind each anterior corner and a very much smaller spine about mid-way down the lateral margin of the carapace. The scutal groove is shallow and restricted to the median surface. There is a pair of small spinous tubercles on the posterior surface of the carapace spaced the width of the scutal groove. The tergal areas are not defined by transverse grooves. Areas 1, 3, and 4 are armed with a median pair of spines of which area 1 are smallest and area 3 largest. The pair of spines on area 4 is widely separated. All areas are also provided with small tubercles arranged in transverse row. Posterior margin of scute and free tergites each with a transverse row of spinous tubercles. Genital operculum smooth.

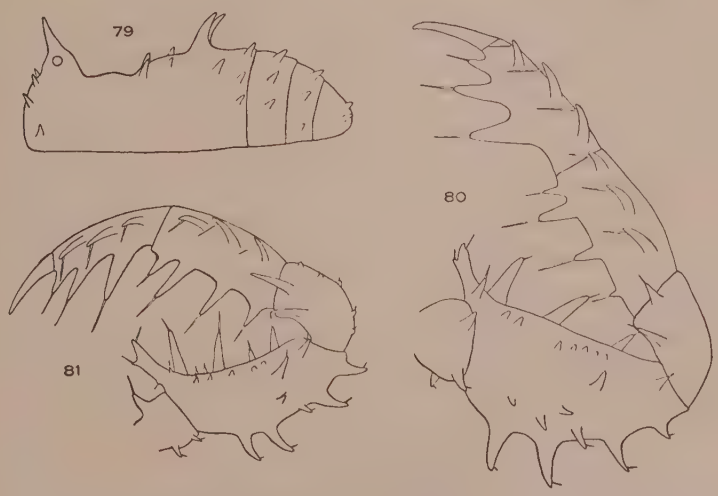


Fig. 79-81.—*Jenolanicus tambourineus* Roewer.
Fig. 79, lateral view of body; Fig. 80, prolateral view of male pedipalp; Fig. 81, prolateral view of female pedipalp.

Chelicerae: Distodorsal surface of basal segment swollen, with a small median tubercle. Second segment with 2 spinous tubercles on the proximodorsal surface.

Pedipalps (*Fig. 81*): There is a pair of strong, elongate spinous tubercles on the proximoventral surface of the femur which are fused at their bases. There are 4 further tubercles along the ventral surface, of which the 1st and 3rd are small. Dorsal surface with 6 strong, spinous tubercles. Tibia with 4 elongate tubercles on retro- and two on proventral margins. Tarsus with 3 on both ventral margins.

Legs: There is a spinous tubercle on the dorsal surface of the trochanter of legs 1 and 2. Coxa 1 is provided with numerous elongate

tubercles along the anteroventral surface. There is a strong, spinous tubercle on the distal retrolateral surface of coxa 2 and the distal prolateral surface of coxa 4. Tarsal formula 3, 8, 4, 4. Distotarsi of legs 1 and 2 is 2 and 3 respectively.

Male

MEASUREMENTS (mm)

Scute: length 3.17, width 3.26

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	1.10	0.44	2.20	0.80	1.59	2.20	1.10	9.43
Leg 2	1.24	0.64	2.91	0.92	3.08	3.96	2.45	15.20
Leg 3	1.15	0.52	2.24	0.97	1.57	2.64	1.41	10.50
Leg 4	1.55	0.65	2.92	1.01	2.61	3.73	1.85	14.32
Pedipalp		0.43	1.98	1.06	1.55		1.15	6.17
			Chelicera: basal 1.10, second 1.45					2.55

Somewhat larger than the female type specimen. The pedipalps are stronger, the femur being more robust. The genitalia are similar to *Jenolanicus altus* (Figs. 85, 86). The calcaneus of the 1st leg is deeply notched. Tarsal formula 5, 11-13, 4, 4.

Types.—Holotype female, Mt. Tambourine, Qld, in Stockholm Museum (seen).

Specimens examined.—QUEENSLAND: National Park (6.xii.1936, J. L. Groom), 1 ♂, 2 ♀♀ (U.Q.); National Park (June 1949), 1 ♂, 4 ♀♀ (U.Q.); McPherson Range, 2500-3850 ft (20.v.51, J. W. T. Armstrong), 2 ♂♂ (A.M.); Mt. Tambourine, under logs and stones (6.v.1953, T. E. Woodward), 2 ♀♀ (C.M.).

Remarks.—It is of importance to note the striking difference in the number of tarsal segments of males and females of both this and the following species.

JENOLANICUS ALTUS, sp. nov.

Figs. 82-86

Holotype Male

MEASUREMENTS (mm)

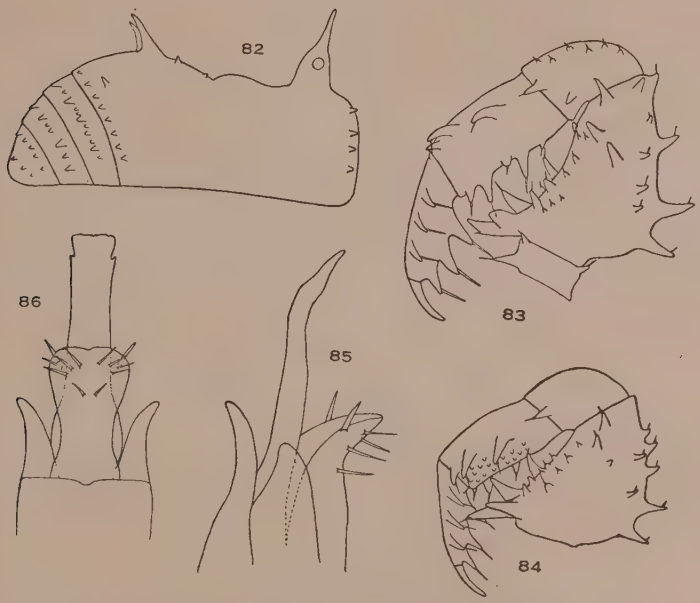
Scute: length 4.85, width 4.40

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	1.32	0.72	2.64	1.10	2.45	2.94	1.76	12.93
Leg 2	1.76	0.88	3.96	1.55	3.97	4.85	3.96	20.93
Leg 3	1.86	0.72	2.62	1.32	2.42	3.36	1.76	14.06
Leg 4	2.48	0.88	3.64	1.41	3.48	5.29	1.95	19.13
Pedipalp		0.68	2.83	1.36	2.19		1.72	8.78
			Chelicera: basal 1.40, second 1.85					3.25

Colour: Body dark reddish brown with few blackish markings on the scute and free tergites. Pedipalps with black reticulate markings. Legs shaded with dark brown.

Body (*Fig. 82*): Eyemound longer than wide in ratio of 3: 2 separated from the anterior margin of the carapace by a distance equal to its length,

and armed with a strong erect apical spine which is equal in height to the eyemound proper. The anterior margin of the carapace is provided with 8 small tubercles. There are no tubercles present behind the anterior corners or on the lateral margins of the carapace. There is a shallow scutal groove which is restricted to the median surface. The tergal areas are not separated by grooves. There is a pair of minute tubercles on the median surface of areas 1 and 2 and a more widely spaced pair on area 4. Area 3 is provided with a strong median pair of spines. Posterior margin of scute and free tergites each with a transverse row of small tubercles.



Figs. 82-86.—*Jenolanicus altus*, sp. nov.
Fig. 82, lateral view of body of male; Fig. 83, prolateral surface of pedipalp of "form *A*" ? male; Fig. 84, prolateral surface of pedipalp of "form *B*" ? male; Fig. 85, lateral view of male genitalia; Fig. 86, ventral view of male genitalia.

Genitalia (*Figs. 85, 86*) : The aedeagus is elongate, flattened dorso-ventrally. Ventral plate with a slight antero-median notch.

Chelicerae : Basal segment with a small tubercle on the mid-distodorsal surface. Second segment with a number of sharp tubercles on the dorsal surface.

Pedipalps (*Figs. 83, 84*) : The pedipalps of the holotype male are as in Figure 83. The tubercle on the proximoventral surface of the femur is provided with a strong blunt secondary process which in the paratype

specimen is much longer and somewhat pointed (Fig. 84). There are further differences in the size and disposition of the tubercles on the femora of these 2 specimens as indicated in the two figures.

Legs: These are sparsely granulate. The calcaneus of the 1st leg is deeply notched. The tarsal formula of the holotype is 6(l.) 5(r.), 11-14, 4, 4, but the tarsal formula of the paratype specimen is 4, 10, 4, 4.

Female

There is a female specimen in the collections of the National Museum of Victoria collected from Tubrabucca, N.S.W., which is possibly of this species, which has 3 segments to tarsus 1.

Types.—Holotype male, Barrington Tops, N.S.W. (Jan. 1925, C. Barrett) ; paratype male, same data (N.M.).

Remarks.—The variation shown between the two specimens available for examination is considerable. It is unfortunate that further material is not available to determine whether the differences shown are dimorphic in character or merely a manifestation of variability within the population. The identical form of the genitalia of the two specimens leaves little doubt that they are indeed a single species. The species is related to *J. tambourineus* Roewer but is clearly separated from it by its larger size, the absence of tubercles behind the anterior corners of the carapace, and the structure of the pedipalps.

Genus MONOXYOMMA Pocock 1903

Monoxyomma manicatum Roewer

Figs. 87-90

Monoxyomma manicata Roewer, 1920, Ark. Zool. 13: 4.
Monoxyomma manicatum Roewer, 1923, Die Weberknechte der Erde, Jena, 608.

Syntype Male

MEASUREMENTS (mm)

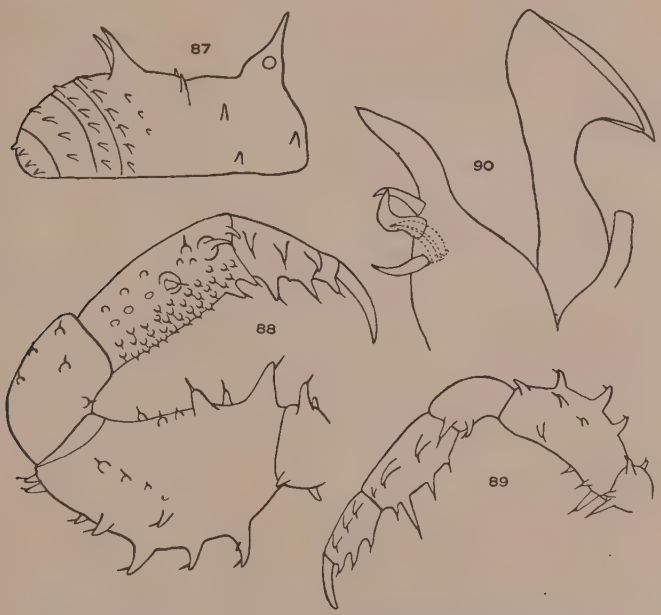
Scute: length 3.30, width 3.17

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	1.32	0.48	2.20	0.88	1.59	1.98	1.15	9.60
Leg 2	2.06	0.66	3.08	0.97	2.73	3.52	3.17	16.19
Leg 3	1.68	0.66	2.43	0.88	1.76	2.20	1.76	11.37
Leg 4	1.76	0.67	2.58	0.88	2.24	3.61	1.89	13.63
Pedipalp		0.57	2.07	1.15	1.59		1.19	6.57
		Chelicera: basal 1.13, second 2.11						3.24

Colour: Ground colour yellowish brown but heavily overlaid with dark brown, the dorsal surfaces of the pedipalps and chelicerae are reticulated.

Body (*Fig. 87*) : The eyemound is separated from the anterior margin of the carapace by a distance equal to one-half of its width. The apical spine is strong and straight, directed slightly forward, equal in length to the height of the eyemound proper. Anterior margin of the carapace with 3 projections, 1 median and 1 at the outer surface of each chelicera.

There are 6 small spines on the carapace, 1 behind each anterior corner, 1 on each mid-lateral margin, and a rather widely separated pair on the median surface. The scutal groove is poorly defined and restricted to the median surface. Tergal areas are not separated by transverse grooves. There is a pair of slender erect spines immediately behind the scutal groove and a very strong pair on the median surface of area 3 (Fig. 87). There is a row of small tubercles on the lateral surfaces of area 4. Posterior margin of the scute and the free tergites with a transverse row of sharp tubercles. Genital operculum smooth.



Figs. 87-90.—*Monoxyomma manicatum* Roewer.
Fig. 87, lateral view of body of male; Fig. 88, prolateral surface of male pedipalp; Fig. 89, prolateral surface of female pedipalp; Fig. 90, lateral view of male genitalia.

Genitalia (*Fig. 90*): Aedeagus large, with a broad flattened apical plate which is sharply pointed laterally. The plate is normally bent in from the median line as shown in Figure 90. The ventral plate is provided with strong setae of which 1 on each margin is curved.

Chelicerae: Basal segment with 2 small dorsal tubercles. Second segment 2 sharp tubercles on proximal dorsal surface.

Pedipalps: These are robust and strongly spined, as shown in Figure 88. The ventral surface of the tibia is covered with rounded pustules and the lateroventral tubercles are represented by only 2 on each distal margin.

Legs: Coxa 1 is armed with 3 elongate tubercles along the anteroventral surface, median longest. There are elongate tubercles on the ventral surfaces of trochanter and femur of leg 1 and the trochanter of leg 4. Tarsal formula 6-7, 14-17, 4, 4. The distotarsi of legs 1 and 2 are 2 and 4 respectively.

Syntype Female

MEASUREMENTS (mm)

Scute: length 3.61, width 3.91

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	1.50	0.53	1.94	0.75	1.98	2.33	1.41	10.44
Leg 2	2.20	0.66	3.08	1.10	3.30	4.18	3.30	17.82
Leg 3	1.89	0.71	2.20	0.88	2.20	2.41	1.76	12.05
Leg 4	2.21	0.79	3.12	0.97	2.42	3.96	2.20	15.67
Pedipalp		0.62	1.98	1.32	3.96		1.32	9.20
			Chelicera: basal 1.10, second 1.94					3.04

Differing from male in the reduced size of the tubercles on the carapace and the pair of tubercles behind the scutal groove. The pedipalps are less robust and are as shown in Figure 89.

Types.—Syntypes, 2 males, 2 females, Evelyne, Qld, in Stockholm Museum (seen). Roewer records six specimens in his original diagnosis and so it is probable that two are housed in the Roewer Collection, Bremen Museum.

Remarks.—The figure given by Roewer (1923) is undoubtedly of a female and not a male as stated in the caption.

MONOXYOMMA ROTUNDUM, sp. nov.

Figs. 91-95

Holotype Male

MEASUREMENTS (mm)

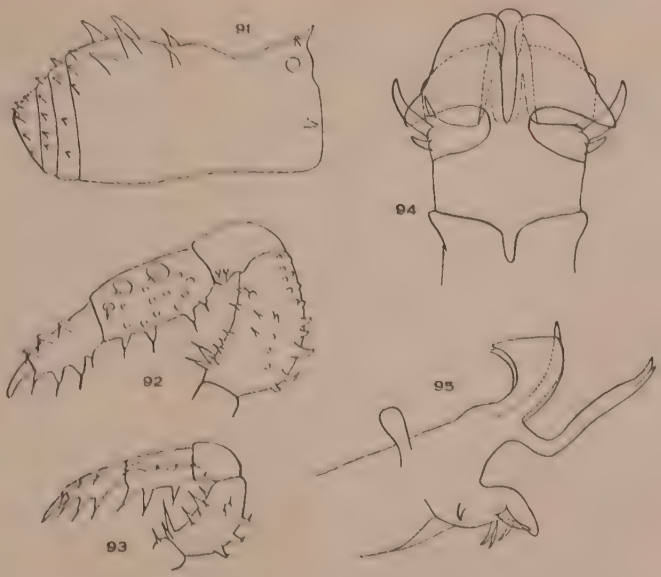
Scute: length 1.76, width 2.20

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.64	0.31	1.32	0.52	0.92	1.19	1.06	5.96
Leg 2	0.97	0.44	1.98	0.56	1.76	1.76	1.98	9.45
Leg 3	0.95	0.39	1.54	0.51	1.15	1.45	0.97	6.96
Leg 4	1.15	0.44	1.80	1.45	0.60	2.20	1.45	9.09
Pedipalp		0.27	1.32	0.64	1.19		0.89	4.31
			Chelicera: basal 0.68, second 1.15					1.83

Colour: Ground colour of body pale yellowish brown. Scute shaded with brown about the eyes and on the mid-lateral and posterior surface of the scute. Free tergites and the sternites heavily shaded with blackish brown. Legs with alternate pale and dark brown patches. Chelicerae and pedipalps with fine black reticulate markings.

Body (*Fig. 91*): The eyemound is large, rounded, rising almost directly from the anterior margin of the carapace, as wide as it is high, with a short apical spine which is equal in length to half of the height of the eyemound proper. The anterior margin of the carapace is smooth.

There is a small tubercle behind each anterior corner. The surface of the carapace behind the eyemound rises slightly. The scutal groove is indicated by a slight depression on the median surface. The tergal areas are not separated by transverse grooves. There is a median pair of spines on areas 1, 3, and 4. The spines on areas 3 and 4 are strong. Posterior margin of the scute and free tergites with small conical tubercles, restricted to the median surface on the posterior margin of the scute. Sternum narrow. Genital operculum smooth.



Figs. 91-95.—*Monoxyomma rotundum*, sp. nov.
Fig. 91, lateral view of body of male; Fig. 92, prolateral surface of male pedipalp; Fig. 93, prolateral surface of female pedipalp; Fig. 94, ventral view of male genitalia; Fig. 95, lateral view of male genitalia with aedeagus extended.

Genitalia (*Figs. 94, 95*): The aedeagus is complex, with a dorsal lamina which is provided with 2 spinous processes and a tubular ventral portion through which the ejaculatory duct passes.

Chelicerae: Basal segment smooth. Second segment with 2 small spinous tubercles on the dorsal surface.

Pedipalps (*Fig. 92*): There are 2 strong tubercles on the proximo-ventral surface of the femur and a number of small tubercles on the ventral, prolateral and distodorsal surfaces. There are 5 sharp tubercles along the proximal half of the dorsal surface.

Legs: There are 4 tubercles on the ventral surface of the 1st femur; legs otherwise sparsely granulate. Calcaneus relatively long, equal to

about one-third of the length of the metatarsus. Tarsal formula 5, 9, 4, 4. Distotarsi of legs 1 and 2 are 2 and 3 respectively.

Allotype Female

MEASUREMENTS (mm)

Scute: length 1.76, width 1.98

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.44	0.27	1.06	0.44	0.72	1.01	0.76	4.70
Leg 2	0.72	0.35	1.70	0.64	1.49	1.55	1.74	8.19
Leg 3	0.71	0.33	1.15	0.44	0.97	1.24	0.92	5.76
Leg 4	0.92	0.44	1.55	0.52	1.15	1.74	0.97	7.29
Pedipalp		0.22	0.72	0.42	0.64		0.52	2.52
			Chelicera: basal 0.52, second 0.97					1.49

Similar to male in appearance. The pedipalps are much smaller and most of the tubercles are relatively longer. The spines on areas 3 and 4 are greatly reduced in size. Tarsal formula 5, 9-10, 4, 4. Distotarsi as in male.

Types.—Holotype male, National Park, south Qld (6.xii.1936, J. L. Groom) ; allotype female, same data; paratypes same data, 2 ♂♂, 1 imm.; holotype male, allotype female (Q.M.), paratypes (A.M., U.Q.).

Genus HETERONUNCIA Roewer 1920

HETERONUNCIA ROBUSTA Roewer

Figs. 96-101

Heteronuncia robusta Roewer, 1920, Arkiv. Zool. Stockholm **13**: 7.
Heteronuncia robusta Roewer, 1923, Die Weberknechte der Erde, Jena, 594.

Lectotype Male

MEASUREMENTS (mm)

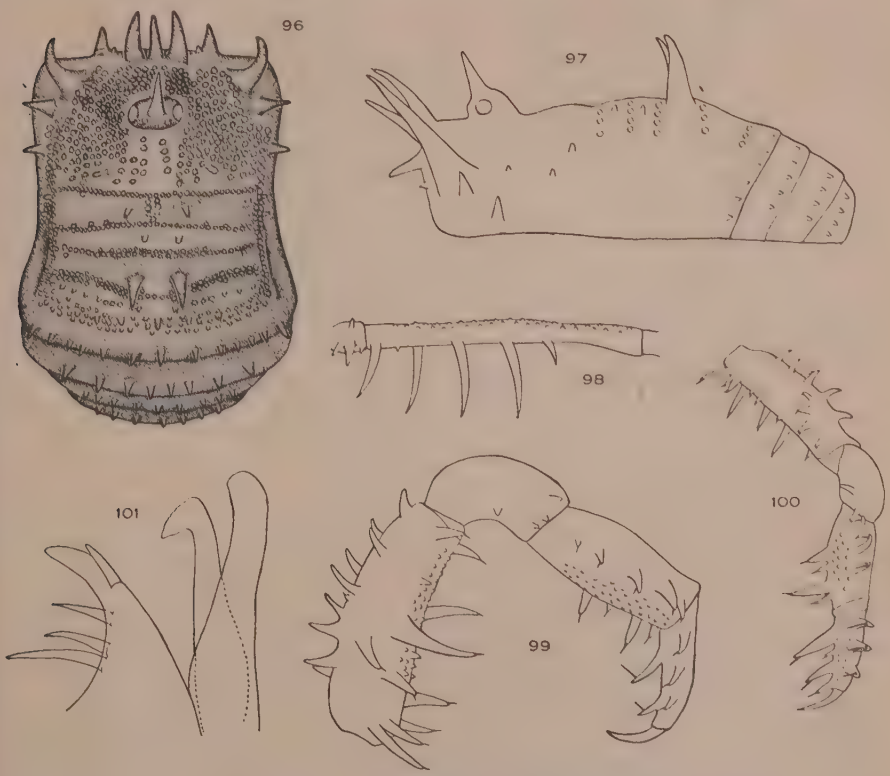
Scute: length 5.73, width 4.85

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	1.76	0.88	3.96	1.32	2.41	4.15	1.21	15.69
Leg 2	2.64	0.97	7.23	1.76	5.73	9.25	3.08	30.66
Leg 3	2.43	0.97	4.85	1.59	3.52	7.93	1.76	23.05
Leg 4	2.85	1.10	7.72	1.71	4.61	11.01	2.20	31.20
Pedipalp		1.32	3.52	1.76	2.64		1.74	10.98
			Chelicera: basal 1.32, second 1.76					3.08

Colour: The body and appendages are pale yellowish brown.

Body (*Figs. 96, 97*) : The eyemound is relatively low, separated from the anterior margin of the carapace by a distance equal to its width, with a slender apical spine, which is equal in length to 3 times the height of the eyemound. The eyemound is smooth apart from a small rounded tubercle behind each eye. There is a group of 3 strong spines near the anterior margin of the carapace in front of the eyemound. These spines are directed obliquely forward and the outer 2 are curved. There is a strong spine on each mid-lateral surface and a further much stronger pair behind each anterior corner. The more anterior spine of this latter pair is strongly curved. The lateral margins of the carapace are armed with a

single small spine near the mid-point. The carapace is closely pustulate. There are rows of pustules down the lateral margins of the tergal region and 4 transverse rows separate the tergal areas. There are 2 small tubercles on the median surface of areas 1 and 2 and a pair of strong spines on the median surface of area 3. The posterior margin of the scute and free tergites each with a transverse row of small conical tubercles. Genital operculum smooth.



Figs. 96-101.—*Heteronuncia robusta* Roewer.
Fig. 96, dorsal surface of body of male; Fig. 97, lateral view of body of male; Fig. 98, trochanter and femur of 1st leg of male; Fig. 99, prolateral surface of male pedipalp; Fig. 100, prolateral surface of female pedipalp; Fig. 101, male genitalia.

Genitalia: Simple, as shown in Figure 101.

Chelicerae: Basal segment with 1 strong sharp distodorsal tubercle, 2 smaller prolateral tubercles, and a stronger proventral tubercle. Second segment with a number of tubercles along the dorsal surface.

Pedipalps: Strong, with massive spinous tubercles on ventral surface of femur (Fig. 99).

Legs: Coarsely granulate, femur 1 with 4-5 strong spines on the ventral surface. Tarsal formula 3, 10-11, 4, 4. Distotarsi of legs 1 and 2 are 2 and 3.

Syntype Female

MEASUREMENTS (mm)

Body: length 4.40, width 4.40

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	1.54	0.66	2.86	1.10	1.94	3.65	0.97	12.72
Leg 2	2.20	0.71	6.61	1.54	5.07	7.05	2.82	26.00
Leg 3	1.98	0.75	4.63	1.10	3.08	6.35	1.23	19.12
Leg 4	2.20	0.88	6.43	1.32	3.74	9.25	1.98	25.80
Pedipalp		0.52	2.20	0.88	1.36		1.32	6.28
			Chelicera: basal 0.92, second 1.59					2.51

Smaller than male. The 3 spines on the anterior median surface of the carapace are greatly reduced in size. Pedipalps less robust, as shown in Figure 100. Femur of leg 1 spined as in male. Tarsal formula and distotarsi as in male.

Types.—Two syntypes, 1 male, 1 female, Malanda, Qld, Mjöberg Collection in Stockholm Museum. I have selected the male specimen as lectotype.

Genus TRIAENOBUNUS Soerensen 1886

TRIAENOBUNUS MINUTUS, sp. nov.

Figs. 102-106

Holotype Male

MEASUREMENT (mm)

Scute: length 1.25, width 1.15

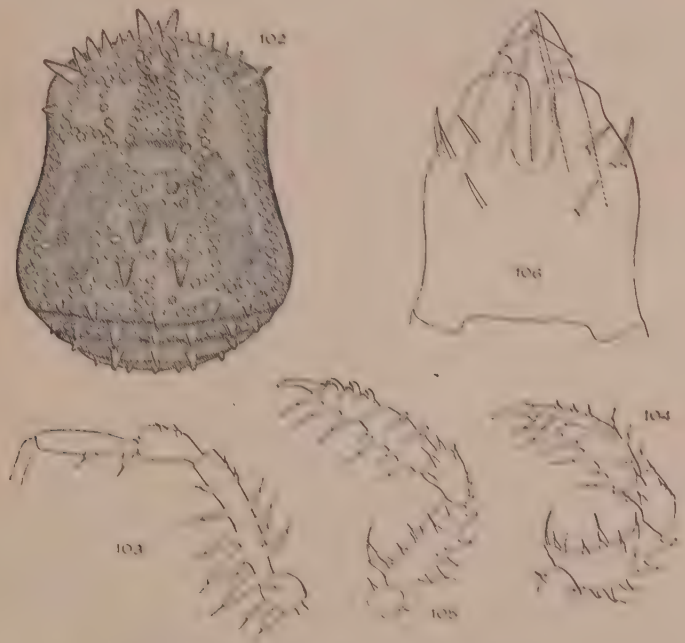
	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.31	0.18	0.53	0.29	0.49	0.38	0.71	2.89
Leg 2	0.53	0.21	1.13	0.38	1.15	1.10	0.56	5.06
Leg 3	0.45	0.21	0.58	0.31	0.54	0.80	0.31	3.20
Leg 4	0.51	0.26	1.00	0.36	0.71	1.36	0.31	4.51
Pedipalp		0.18	0.92	0.29	0.31		0.26	1.96
			Chelicera: basal 0.18, second 0.39					0.57

Colour: Ground colour of body deep orange-brown with a black patch on each side of the tergal region. Sternites with 3 black areas. Appendages heavily shaded with brown.

Body (*Fig. 102*): Eyemound with a stout median spine, which is directed obliquely forward over the anterior margin of the carapace. There are 2 further spinous processes directed forward from base of the anterior surface of the eyemound. There are 5 spinous tubercles along the anterior margin of the carapace each side of the eyemound and a single stronger tubercle behind each anterior corner. The scutal groove is indistinct and restricted to the median surface. The dorsal pattern is not well defined and is composed of relatively large pustules. There is a small median pair of tubercles on areas 2-4, more widely spaced on area 4.

Posterior margin of scute and free tergites armed with a transverse row of conical tubercles. Sternum broad. Genital operculum smooth.

Genitalia (*Fig. 106*): There are 3 stout spinous processes extending beyond the tip of the aedeagus. Ventral plate with a median incision extending to almost half of its length, provided with 2 groups of 4 small setae.



Figs. 102-106.—*Triaenobunus minutus*, sp. nov.
Fig. 102, dorsal surface of body of male; Fig. 103, leg 1 of male; Fig. 104, prolateral surface of male pedipalp; Fig. 105, prolateral surface of female pedipalp; Fig. 106, male genitalia.

Chelicerae: Basal segment smooth. Second segment with 3 small tubercles on the dorsal surface.

Pedipalps (*Fig. 104*): There are 5 strong spinous tubercles on the dorsal surface of the femur. Ventral surface with 2 strong proximal tubercles, proventral unevenly bifid, a strong tubercle on the mid-retroventral surface and 4 smaller tubercles on the proventral surface. Tibia with 2 strong tubercles on both ventral margins. Tarsus with 3 on both ventral margins. There is a prominent lobe on the retrolateral margin of coxa 2 and the prolateral margin of coxa 4.

Legs: First leg with tubercles on the ventral surface of the trochanter, dorsal and ventral surfaces of the femur, and ventral surface of tibia (Fig. 103). Legs otherwise granulate but without tubercles. Tarsal formula 3, 4, 4, 4. Distotarsi of legs 1 and 2 are 2 and 3 respectively.

Female

MEASUREMENTS (mm)

Scute: length 1.41, width 1.31

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.31	0.15	0.56	0.31	0.41	0.32	0.65	2.71
Leg 2	0.54	0.18	1.17	0.36	1.15	1.10	0.52	5.02
Leg 3	0.45	0.18	0.72	0.31	0.53	0.79	0.29	3.27
Leg 4	0.54	0.26	1.05	0.33	0.74	1.36	0.29	4.57
Pedipalp		0.17	0.51	0.26	0.28		0.23	1.45
			Chelicera: basal 0.17, second 0.36					0.53

Differing from the male in minor characters of the pedipalps (Fig. 105), the femur is more slender and the bifid proximoventral tubercle of the male is represented by 2 separate tubercles. Tarsal formula as in male.

Types.—Holotype male, allotype female, Binna Burra, south Qld, from leafmould (4.ix.1952, T. E. Woodward) (Q.M.).

Triaenobunus armstrongi, sp. nov.

Figs. 107-109

Holotype Female

MEASUREMENTS (mm)

Scute: length 1.62, width 1.76

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.48	0.27	0.44	0.39	0.45	0.43	0.31	2.77
Leg 2	0.66	0.22	0.69	0.44	0.75	0.81	0.44	4.01
Leg 3	0.53	0.26	0.53	0.35	0.48	0.62	0.35	3.12
Leg 4	0.88	0.26	0.79	0.43	0.76	1.22	0.35	4.69
Pedipalp		0.14	0.53	0.32	0.44		0.32	1.75
			Chelicera: basal 0.27, second 0.53					0.80

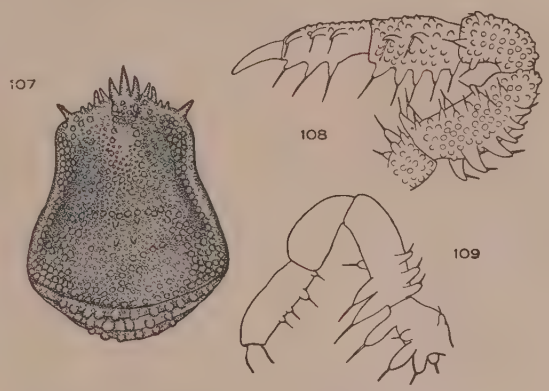
Colour: The ground colour of the body is pale yellowish brown, but there is heavy black shading over most of the scute and free tergites. Pedipalps and chelicerae pale yellow-brown. Legs yellow brown but with dark bands.

Body: The eyemound is low, only slightly raised above the surface of the carapace, with 3 strong spines directed horizontally forward from the anterior margin. The entire body including the pedal coxae and the genital operculum is closely covered with small granules. There is also a scutal pattern of larger granules as shown in Figure 107. Anterior margin of the carapace, each side of the eyemound, with 4 spines of which the inner pair are larger. There is a further strong spine on each anterior corner of carapace. Scutal groove absent. Sternum broad, typical.

Chelicerae: Small, with small tubercles on dorsal surfaces of both segments.

Pedipalps (*Fig. 108*): All segments are covered with small pustules, ventral surface of tarsus smooth. Trochanter with 1 strong and 3 small tubercles on ventral surface. Femur with row of 6 strong spinous tubercles

on dorsal surface; 2 large and 1 small proximoventral tubercles, and number of small tubercles on the ventral and prolateral surfaces. Patella with 3 distal tubercles, 1 ventral, 1 prolateral, and 1 dorsal in position. Tibia with 2 pro- and 4 retroventral tubercles. Tarsus with 3 tubercles on both pro- and retroventral surfaces.



Figs. 107-109.—*Triaenobunus armstrongi*, sp. nov. Fig. 107, dorsal surface of body of female; Fig. 108, prolateral surface of pedipalp; Fig. 109, leg 1 of female.

Legs: Trochanter, femur, and tibia with strong tubercles as shown in Figure 109. Legs otherwise finely granulate. Tarsal formula 2, 2, 3, 3.

Types.—Holotype ♀, Spencer Creek, Mt. Kosciusko, N.S.W. (28.xi.1952, J. W. Armstrong) (A.M.).

Triaenobunus woodwardi, sp. nov.

Figs. 110-112

Holotype Female

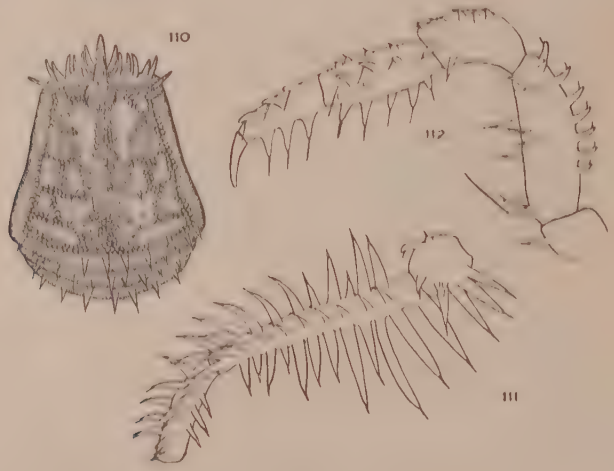
MEASUREMENTS (mm)

Scute: length 1.95, width 1.95

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.57	0.31	1.06	0.44	0.75	0.75	0.32	4.20
Leg 2	0.88	0.27	1.54	0.57	1.41	1.76	0.57	7.00
Leg 3	0.71	0.30	1.01	0.43	0.88	1.29	0.44	5.06
Leg 4	0.88	0.35	1.55	0.44	1.10	1.98	0.45	6.75
Pedipalp		0.18	0.79	0.39	0.48		0.39	2.23
				Chelicera: basal 0.35, second 0.66				1.01

Body: Eyemound low, with strong median spinous process, directed forward and with 3 tubercles on dorsal surface and 2 pairs of strong lateral branches. Anterior margin of the carapace with 4 spines each side of eyemound grouped in 2 pairs, and pair behind each anterior corner, of which the more anterior one is larger. The scutal pattern is formed with

small pustules and is shown in Figure 110. There are 2 rows of small spinous tubercles extending back from the posterior margin of the eye-mound to the scutal groove. The scutal groove is shallow and only faintly visible. The tergal areas are not defined by transverse grooves. Areas 1-3 with conical tubercles, 2, 4, and 6 respectively. Posterior margin of scute and free tergites armed with sharp conical tubercles. Sternum broad posteriorly. Genital operculum with few setose pustules grouped mainly on the anterior surface.



Figs. 110-112.—*Triaenobunus woodwardi*, sp. nov. Fig. 110, dorsal surface of body of female; Fig. 111, first leg of female; Fig. 112, prolateral surface of female pedipalp.

Chelicerae: Small, smooth, with few small tubercles on the dorsal surfaces of both segments.

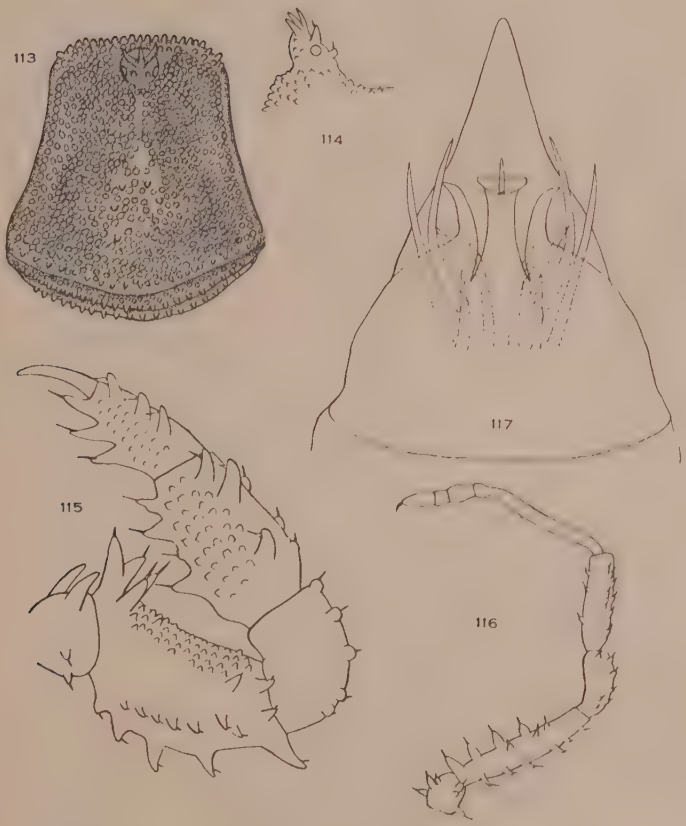
Pedipalps (*Fig. 112*): Weak. Femur with a row of 7 spinous tubercles along the dorsal surface, 3 elongate tubercles on the proximoventral surface of which the more proximal is provided with a long apical seta equal in length to twice that of the tubercle itself. There are further tubercles on the mid-ventral and distal prolateral surfaces. Patella with tubercles on the dorsal and distal prolateral surfaces. Tibia with 5 retro- and 3 proventral tubercles. Tarsus with 3 tubercles on both ventral margins.

Legs: Trochanter, femur, patella, and tibia of all legs armed with strong elongate, spinous tubercles arranged dorsoventrally. More prominent on leg 1 (Fig. 111). Tarsal formula 3, 5, 4, 4. Distotarsi of legs 1 and 2 are 2 and 3 respectively.

Type.—Holotype female, Mt. Tambourine, east side below Eagle Point, from leafmould (8.v.1953, T. E. Woodward) (Q.M.).

Triaenobunus pescotti, sp. nov.

Figs. 113-117



Figs. 113-117.—*Triaenobunus pescotti*, sp. nov.
Fig. 113, dorsal surface of body of male; Fig. 114, lateral view of eyemound; Fig. 115, prolateral surface of male pedipalp; Fig. 116, first leg of male; Fig. 117, male genitalia.

Holotype Male

MEASUREMENTS (mm)

Scute: length 2.84, width 2.83

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.86	0.31	1.32	0.53	0.88	1.15	0.53	5.58
Leg 2	1.32	0.44	1.76	0.75	1.69	2.20	1.14	9.30
Leg 3	1.20	0.43	1.15	0.66	1.15	1.98	0.66	7.23
Leg 4	1.29	0.44	1.85	0.79	1.54	2.24	0.83	8.98
Pedipalp		0.27	0.97	0.53	0.71		0.39	2.87
Chelicera: basal 0.88, second 0.79								1.67

Colour: The scute, free tergites, sternites, and all segments of the legs, except the trochanters, are black. The chelicerae, pedipalps, and the trochanters of all legs are pale creamy-yellow.

Body: The eyemound is high, subconical, directed obliquely forward with 3 apical spinous processes (Figs. 113). Anterior margin of the carapace without spines. Scute closely covered with pustules which do not form a pattern. Scutal groove only faintly visible. Areas not defined and without spinous tubercles. Posterior margin of the scute and free tergites with small tubercles. Sternum broad. Genital operculum sparsely covered with minute pustules.

Genitalia are as shown in Figure 117.

Chelicerae: There is a small tubercle on the distodorsal surface of the basal segment and a row of from 4-5 along the dorsal surface of the 2nd segment.

Pedipalps (*Fig. 115*): The ventral surfaces of the femur, tibia, and tarsus are granulate. There is a strong bifid tubercle on the proximoventral surface of the femur with 2 further tubercles slightly anterior. Dorsal surface with 2 longitudinal rows of tubercles, retrodorsal row stronger. Tibia and tarsus with 3 spinous tubercles on both pro- and retroventral margins.

Legs: First leg with elongate tubercles on trochanter and femur (Fig. 116). Legs otherwise granulate. Tarsal formula 3, 6, 3, 3. Distotarsi of legs 1 and 2 are 2 and 3.

Type.—Holotype male, Tubrabucca, N.S.W. (16.i.1948, R. T. M. Pescott, A. N. Burns) (N.M.).

Triaenobunus groomi, sp. nov.

Figs. 118-122

Holotype Male

MEASUREMENTS (mm)

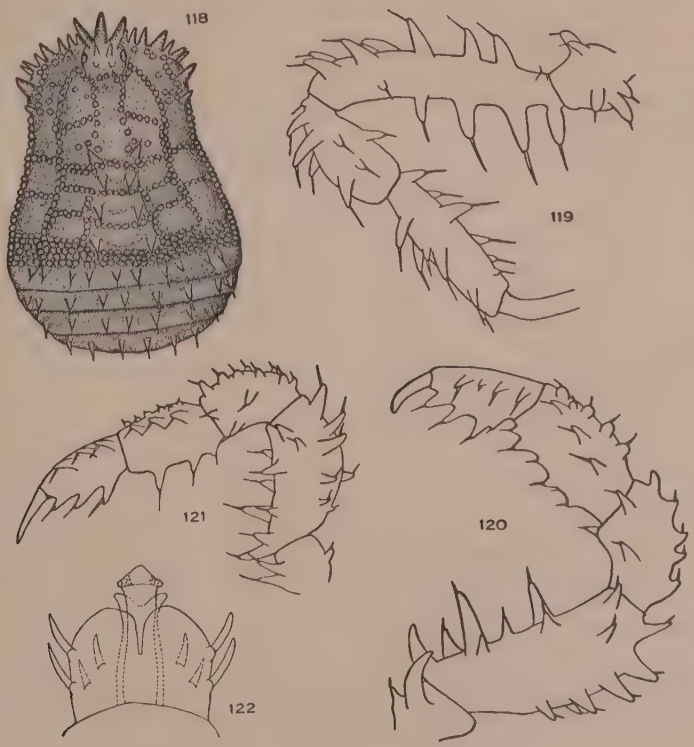
Scute: length 2.20, width 1.99

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.56	0.32	0.92	0.39	0.56	0.88	0.35	3.98
Leg 2	0.92	0.35	1.54	0.48	1.24	1.85	0.92	7.30
Leg 3	0.72	0.27	0.97	0.44	0.76	1.15	0.56	4.87
Leg 4	1.06	0.44	1.36	0.45	1.15	1.86	0.60	6.92
Pedipalp		0.39	0.72	0.44	0.44		0.35	2.34
Chelicerae: basal 0.48, second 0.76								1.24

Colour: Dorsal surface of body dark reddish brown, ventral surface pale yellowish brown. Dorsal surfaces of chelicerae and pedipalps with dark reticulate markings. Leg with alternate pale and dark brown bands.

Body: The eyemound is well developed, granulate, with a trident of 3 equally developed spines on the anterodorsal surface, which are directed forward over the anterior margin of the carapace. There is a row of from 6-7 spinous tubercles along the anterior margin of the carapace each side

of the eyemound and 2 on each lateral margin of the carapace, of which the anterior is the stronger. Scute with a pattern of small pustules arranged as in Figure 118. Scutal groove shallow, restricted to the median surface. Tergal areas not defined by transverse groove, but with 4 median pairs of relatively strong conical tubercles; anterior pair directed forward. Posterior margin of the scute and free tergites each with a transverse row of similar tubercles. Genital operculum smooth. Sternum narrow and elongate but widening posteriorly.



Figs. 118-122.—*Triaenobunus groomi*, sp. nov.
Fig. 118, dorsal surface of body of male; Fig. 119, first leg of male; Fig. 120, prolateral surface of male pedipalp; Fig. 121, prolateral surface of female pedipalp; Fig. 122, male genitalia.

Genitalia are as shown in Figure 122. The aedeagus is slender, with a distal cap which is somewhat denticulate. Ventral plate entire but with a deep median notch.

Chelicerae: Small. Basal segment with a single spinous tubercle on the distodorsal surface. Second segment with 2 small dorsally situated tubercles.

Pedipalps (*Fig. 120*): Trochanter with 2 ventral tubercles of which the inner is strong and curved forward. Femur with 7 ventral tubercles, of which 3 proximal and 1 distal are strong; dorsal surface with 6 spinous tubercles grouped on distal half of the segment and with 2 small distal prolateral tubercles. Patella and tibia with numerous small tubercles on the dorsal surface. Patella with 2 prolateral and 1 ventral tubercles. Tibia with 3 pro- and 5 retroventral tubercles. Tarsus with 3 spinous tubercles on both ventral margins.

Legs: There is a strong spinous tubercle on the retrolateral surface of coxa 2 and the prolateral surface of coxa 4. All segments, except the metatarsi and tarsi, are strongly tuberculate, strong on leg 1 (Fig. 119). Calcaneus short. Tarsal formula 3, 7, 4, 4. Distotarsi of legs 1 and 2 are 2 and 3 respectively.

Allotype Female

MEASUREMENTS (mm)

Scute: length 2.03, width 1.86

	Cox.	Troch.	Fem.	Pat.	Tib.	Met.	Tars.	Total
Leg 1	0.61	0.26	0.77	0.42	0.56	0.66	0.42	3.70
Leg 2	0.92	0.31	1.26	0.51	1.10	1.55	0.77	6.42
Leg 3	0.77	0.26	0.82	0.36	0.72	1.05	0.46	4.44
Leg 4	0.94	0.36	1.20	0.51	0.93	1.70	0.61	6.25
Pedipalp		0.26	0.56	0.31	0.33		0.36	1.82
		Chelicera: basal 0.36, second 0.51						0.87

Similar in structure to male. Pedipalp more slender than male, as shown in Figure 121. Legs less strongly tuberculate.

Types.—QUEENSLAND: Holotype male, allotype female, National Park, Qld (6.xii.1936, J. L. Groom), paratypes 1 ♂, 1 ♀, Binna Burra, Lamington Plateau, Qld, ex leafmould (28.viii.1953, T. E. Woodward). Holotype ♂, allotype ♀ (Q.M.), paratypes (A.M., C.M.).

Remarks.—By virtue of the narrow sternum the species described above should be placed, under the existing classification, into the Triaenonychini. However, apart from the shape of the sternum it appears to be a typical *Triaenobunus* species and I do not feel inclined to establish a new genus for it as would be necessary if it were transferred.

Acknowledgments

I am deeply indebted to Dr. T. E. Woodward, Entomology Department, University of Queensland, for the numerous specimens he has forwarded which included many new and interesting species. I am also indebted to Dr. Woodward for arranging the loan of material held in the Entomology Department of the University of Queensland.

I am indebted to Mr. J. W. T. Armstrong for specimens collected from New South Wales. Through the kindness of Dr. A. B. Walkom, Director, Australian Museum, I have been able to examine the collection housed in the museum.

I am most grateful for the trust shown by Dr. René MaLaise, Stockholm Museum, Dr. A. Kaestner and Dr. G. Steinbach, Zoological Museum, Berlin, and Dr. H. Weidner, Hamburg Museum, who forwarded to me for examination types of Australian Opiliones housed under their care.

References

Forster, R. R. (1949).—Australian Opiliones. Mem. Nat. Mus. Melb. No. 16: 59-89.

Forster, R. R. (1954).—The New Zealand harvestmen (Suborder Laniatores). Canterbury Mus. Bull. No. 2: 1-329.

Goodnight, C. J., and Goodnight, M. L. (1948).—New phalangids from the south-west Pacific. Amer. Mus. Novit. No. 1371.

Karsch, F. (1880).—Arachnologische Blätter. *Z. ges. Naturw.* 53: 373-409, pl. XII.

Roewer, C. Fr. (1912).—Die Familien der Assamiden und Phalangodin der Opiliones—Laniatores. *Arch. Naturgesch.* A 78 (3): 1-242.

Roewer, C. Fr. (1920).—Results of Dr. E. Mjöberg's Swedish scientific expedition to Australia, 1910-13. XXIV. Australische Opiliones *Ark. Zool.* 13 (8): 1-10, 1 pl.

Roewer, C. Fr. (1923).—Die Weberknechte der Erde: Systematische Bearbeitung der bisher bekannten Opiliones. pp. VI+1116, 1212 figs.

Roewer, C. Fr. (1935).—Alte und neue Assamiidae Weitere Weberknechte. VIII. Ergänzung der "Weberknechte der Erde" 1923 *Veröff. Dtsch. KolonMus. Bremen* 1 (1): 1-168, 9 pl.

Soerensen, W. (1886).—Opiliones in Koch's Arachniden Australiensis. XXXIII.

Sorensen, W. (1932).—Descriptiones laniatorum (Arachnidorum Opilionum Subordinis) fecit William Soerensen opus posthumum recognovit et editit Kai. L. Henriksen, *Mém. Acad. Roy. Sci. Lettres, Copenhagen*, Ser. 913 (4): 199-422.

List of Genera and Species

THE ACARINA FAUNA OF MUTTON BIRDS' NESTS ON A BASS STRAIT ISLAND*

By H. WOMERSLEY†

(*Manuscript received March 29, 1955*)

Summary

A collection of Acarina inhabiting the nests of the mutton bird, *Puffinus tenuirostris* Temminck, on Fisher I., Bass Strait, is described. Fourteen species, belonging mainly to the Mesostigmata are described or recorded of which two genera *Laelapsella* and *Austruropoda*, and six species *Hypoaspis acme*, *Laelapsella humi*, *Gymnolaelaps annectans*, *Austruropoda tasmanica*, *Variatipes longisetosus*, and *Acroglyden* (*Cosmoglyphus*) *mykytowyczi* are new, *Haemolaelaps australis* Berlese 1910 is now redescribed in the female sex after a comparison of the type in the Berlese collection in Florence. The male is described for the first time.

Of the species found *Hypoaspis acme*, *Laelapsella humi*, *Gymnolaelaps annectans*, *Haemolaelaps glasgowi*, and *Mesolaelaps australiensis* can be considered to be ectoparasites and the remainder, except *Zachvatkinia puffini* which is a true feather mite, are detritus and excreta feeders.

INTRODUCTION

During January 1953 Dr. R. Mykytowycz of the Wildlife Survey Section, C.S.I.R.O., made a survey of the habits of the mutton bird, *Puffinus tenuirostris* Temminck, on Fisher I. in Bass Strait, Australia. He was able to collect a number of mites from the nesting material and from the burrows inhabited by the birds. Apart from these specimens which he forwarded to me for study, he also sent quantities of the nesting material and debris which were later put through the Berlese funnel and further mites were thus obtained. Altogether 14 species are described or recorded in this paper, two genera and a number of species being new.

Of the species found five *Hypoaspis acme*, sp. nov., *Laelapsella humi*, gen. et sp. nov., *Gymnolaelaps annectans*, sp. nov., *Haemolaelaps glasgowi* Ewing, and *Mesolaelaps australiensis* Hirst, on the structure and habits of allied forms, may be considered as ectoparasites of the birds. All the other species, except *Zachvatkinia puffini* (Buchholz) which is a true feather mite found on the birds themselves, are typical detritus and excreta inhabitants.

To Mr. F. Ratcliffe, Officer-in-Charge, Wildlife Survey Section, and to Dr. Mykytowycz, I am indebted for the opportunity of studying this interesting material.

Where sufficient material permits, paratypes will be deposited in other museums with acarological collections, and in the collections of the Division of Entomology, C.S.I.R.O.

* This study was assisted in part by a grant from the Trustees of the Science and Industry Endowment Fund, C.S.I.R.O.

† South Australian Museum, Adelaide.

Suborder **MESOSTIGMATA** G. Canestrini 1819

Superfamily **GAMASIDES** Leach 1815

Family **MACROCHELIDAE** Vitzthum

Vitzthum, H., 1930, Zool. Jb. Abt. f. Systematik, Bd. 59.

Genus MACROCHELES Latreille

Latreille, 1829, Cuvier, Reg. Anim. (2nd Ed.) 4: 282.

Type species *Acarus muscae* Scopoli 1772 = *Acarus marginatus* Hermann 1804.

Subgenus NOTHROHOLASPIS Berlese

Berlese, A., 1918, Redia 13: 169.

Type species *Holostaspis tridentatus* G. & R. Canestrini 1882.

MACROCHELES (NOTHROHOLASPIS) ?MONTIVAGUS Berlese

Fig. 1*A-D*

Holostaspis montivagus Berlese, 1887, Acari Myriopoda et Scorpiones Italia Reperta. fasc. 44: No. 4.

Nothroholaspis ?montivagus (Womersley), 1942, Trans. Roy. Soc. S. Aust. 66 (2): 168, fig. 18, A-E.

Fig. 1.—*Macrocheles* (*Nothroholaspis*) *?montivagus* Berl.
Male: *A*, ventral view; *B*, tectum; *C*, chelicerae; *D*, femur of leg II.

Specimens from South Australia and Western Australia, found under boards and rubbish on cultivated land were referred to this species with a query in 1942, and figures given of the female.

Seventeen females and three males were obtained from the nesting material in the burrows by means of the Berlese funnel in January 1953 (coll. R. Mykytowycz).

Like many species of Macrochelidae these mites are not parasitic, but probably coprophilous in habit, feeding on the excreta amongst the nest debris.

As the male has not previously been known it is described and figured.

Male Allotype

Strongly chitinized brownish species. Oval in shape. Length of idiosoma 585 μ, width 416 μ. Dorsal shield not entirely covering dorsum, 580 μ long by 390 μ wide, widest on level of coxae III, with fine reticulate hexagonal lines, except in middle where the markings are as in female; setae fairly thick, bushy with ciliations as typical of genus, to 45 μ long. Ventrally the sternal and genital shields united, and posteriorly narrowly separated from the rounded and expanded ventri-anal shield which is 216 μ wide by 190 μ long, a small metapodal shield on each side, all shields with reticulate markings as in female; sternal setae to 42 μ, ventri-anal setae to 22 μ, setae lateral of ventri-anal to 14 μ. Chelicera as figured, movable finger with 1 strong tooth and a long 106 μ, doubly flexed spermatophore carrier, fixed finger with 1 small distal tooth and a large more basal tooth. Tectum as figured, the basal arms not pointed as in female but with 3-4 apical fibriles. Leg I long, 494 μ and slender, without tarsal claws; II thicker, 494 μ long, with a strong thumb-like apophysis ventrally on genu, and a much smaller one on tibia; III strong as in II, 455 μ; IV strong and the longest, 650 μ; legs II-IV with paired claws and caruncle; coxae all without spines or armature.

Remarks

The allotype and two paratype males in the collection of the South Australian Museum.

Family **LAELAPTIDAE** Berlese

Berlese, A., 1892, Acari Myriopoda et Scorpiones Italia Reperta fasc. 14: No. 30.

Subfamily **HYPOASPIDINAE** Vitzthum

Vitzthum, H., 1941, Acari *in* Bronn's Tierreich, 5: 762.

Genus HYPOASPIS Canestrini

Canestrini, G., 1885, Atti Ist. Veneto 2 (6): 1369.

Type species *Laelaps krameri* G. & R. Canestrini 1881.

Hypoaspis acme, sp. nov.

Fig. 2*A-F*

Female Holotype

Rather lightly chitinized. Shape oval. Length of idiosoma 845 μ, width 442 μ. Dorsal shield almost entirely covering the dorsum; with only a narrow band of cuticle externally from shoulders, lightly reticulate, with

c. 68 simple setae to 52 μ long and a number of pores, lateral margins of body with setae to 32 μ long. Venter: tritosternum with ciliated laciniae; in front of sternum with irregular pre-endopodal shields strongly pitted;

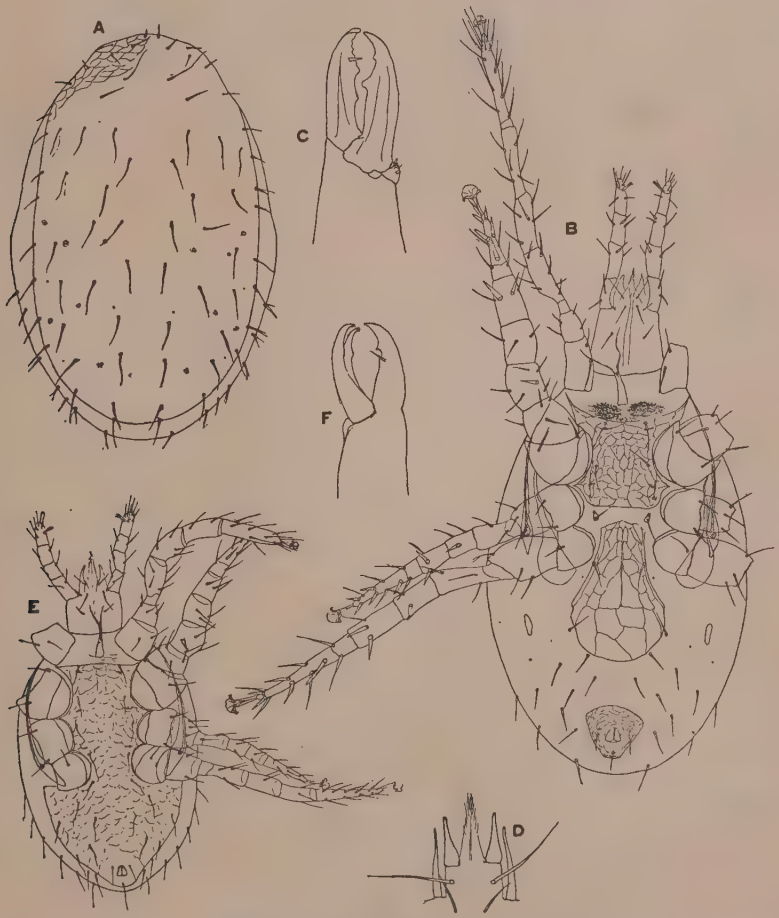


Fig. 2.—*Hypoaspis acme*, sp. nov.
A-D, female: *A*, dorsum; *B*, ventral view; *C*, chelicerae; *D*, gnathosoma; *E-F*, male: *E*, ventral view; *F*, chelicerae.

sternal shield as figured, 162 μ long in medial line, and 260 μ wide between the apices of anterior corners, with 3 pairs of simple setae, 52, 52, and 45 μ long, and with 2 pairs of pores, reticulate, posterior margin almost straight, anterior margin concave; metasternal shields distinct, small, with pore and seta; genitoventral shield flask-shaped, reticulate, with round anterior and posterior ends, with 1 pair of setae 45 μ long, length of shield 273 μ,

width 195 μ, separated from anal shield by 195 μ and with 2 pairs of setae between; anal shield as figured 234 μ long by 221 μ wide, with 3 setae 32 μ long, the pair of anterior setae in line with front of anus; metapodal shields small but distinct, elongate 45 μ by 13 μ; on the cuticle posterior of genitoventral plate 11 pairs of setae; peritreme elongate, with stigma situated between coxae III and IV and the peritremal shield separated narrowly from the exopodal shield which is expanded behind coxae IV. Palpi normal, sensory seta on tarsus with 2 tines. Chelicerae are as figured, the seta on the fixed finger short and stoutish. Legs: generally long and slender, with II the stoutest, I 820 μ long, II 610 μ, III 520 μ, IV 800 μ; no stout spines on coxae or on leg II; tarsi furnished with fairly long caruncle and paired claws.

Male Allotype

As in the female but smaller. Length of idiosoma 360 μ, width 264 μ. Dorsal shield as in female with fine setae to 36 μ long. Venter: all the sternal, genital, ventral, and anal shields united into a single holoventral shield, sternogenital portion with 5 pairs of setae; ventri-anal portion with 5 pairs of setae to 32 μ, and expanded behind coxae IV to 168 μ wide. Legs as in female: I 338 μ long, II 273 μ, III 260 μ IV 358 μ; coxae unarmed, leg II with a single spine on ventral surface of femur, only a little stronger than the setae and similar to that in female. Chelicerae are as figured, fixed finger with 1 tooth and short seta (pilus dentarius) and movable finger with 1 blunt tooth and a strong spermatophore carrier of its own length.

Locality and Host

Described from a single female and 3 male specimens from nesting material in burrows of the mutton bird, *Puffinus tenuirostris,* from Fisher I., Bass Strait, Australia, January 1953 (coll. R. Mykytowycz).

Remarks

This species differs from any other species known to me mainly in the ventral shields of the female. The type and paratype slides of the specimens are in the collection of the South Australian Museum.

Genus LAELAPSELLA, gen. nov.

Dorsal shield entire. In female without jugular or pre-endopodal shields, sternal shield with 3 pairs of setae and 2 pairs of pores; metasternal shields represented by seta; genitoventral shield flask-like, expanded behind coxae IV and reaching to anal shield, with 7 or 8 marginal and submarginal long setae; 3 metapodal shields on each side; anal shield triangular with 3 setae; coxae II and III with strong anterior spines. Dorsal setae are long and tapering. Male as in female, but the holoventral shield widely expanded behind coxae IV and with 12 pairs of setae excluding those between coxae and the anal setae; anterior spines on coxae II and III not so strong as in female.

Type species *Laelapsella humi,* sp. nov.

In the shape of the genitoventral shield of the female this genus is intermediate between *Laelaspis* Berlese and *Gymnolaelaps* Berlese. It differs, however, in having more than 4 pairs of genitoventral setae, and in this respect resembles the genera *Haemogamasus* Berlese, *Euhaemogamasus* Ewing, and *Ischyropoda* Keegan, but it has not the rich pelage of short setae of these genera or the accessory sternal or anal setae of the first and last of these. It seems therefore necessary to establish a new genus.

LAELAPSELLA HUMI, sp. nov.

Fig. 3*A-C*, Fig. 4*A-D*

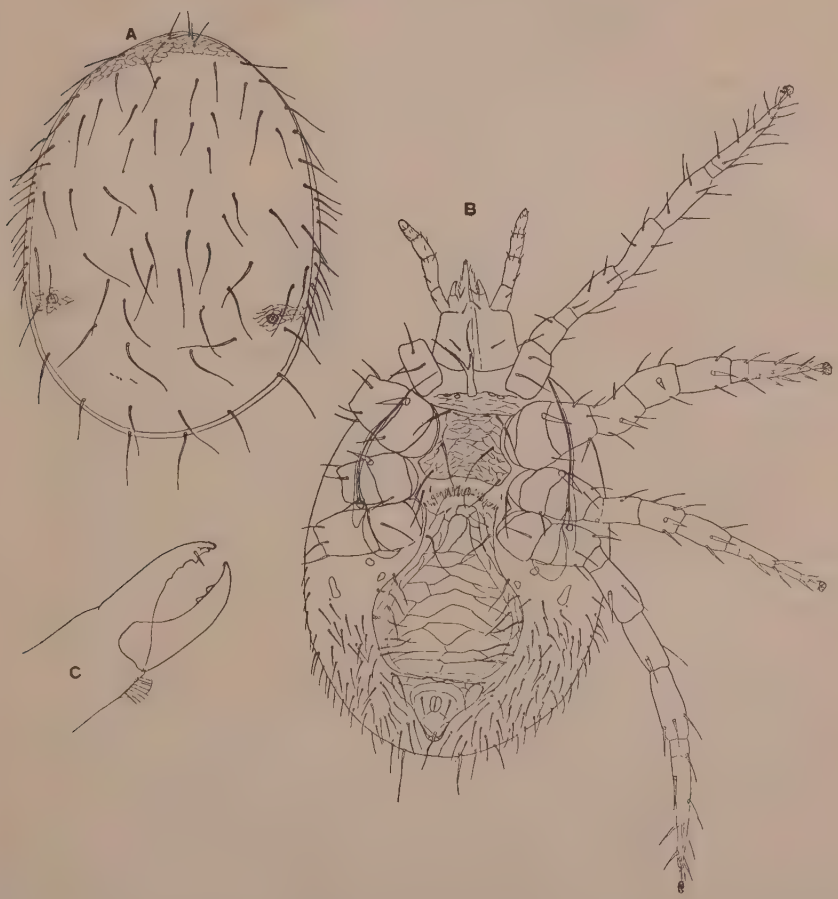


Fig. 3.—*Laelapsella humi*, gen. et sp. nov.
Female: *A*, dorsum; *B*, ventral view; *C*, chelicerae.

Female Holotype

Shape ovoid, widest behind coxae IV. Lightly chitinized. Length of idiosoma 520 μ, width 325 μ. Dorsal shield entire, not wholly covering

dorsum, lightly reticulate, furnished with *c.* 34 pairs of long simple setae to 130 μ long. Venter: cuticle between base of tritosternum and anterior margin of sternal shield with transverse striations, no pre-endopodal or jugular shields present; sternal shield wider than long, reticulate, with 3 pairs of setae and 2 pairs of pores, and posterior margin lightly concave and reaching mid-line of coxae III; metasternal shields only represented by setae and pores; genitoventral shield drop- or flask-like, only slightly expanded behind coxae IV and furnished with 4 pairs of setae, its posterior

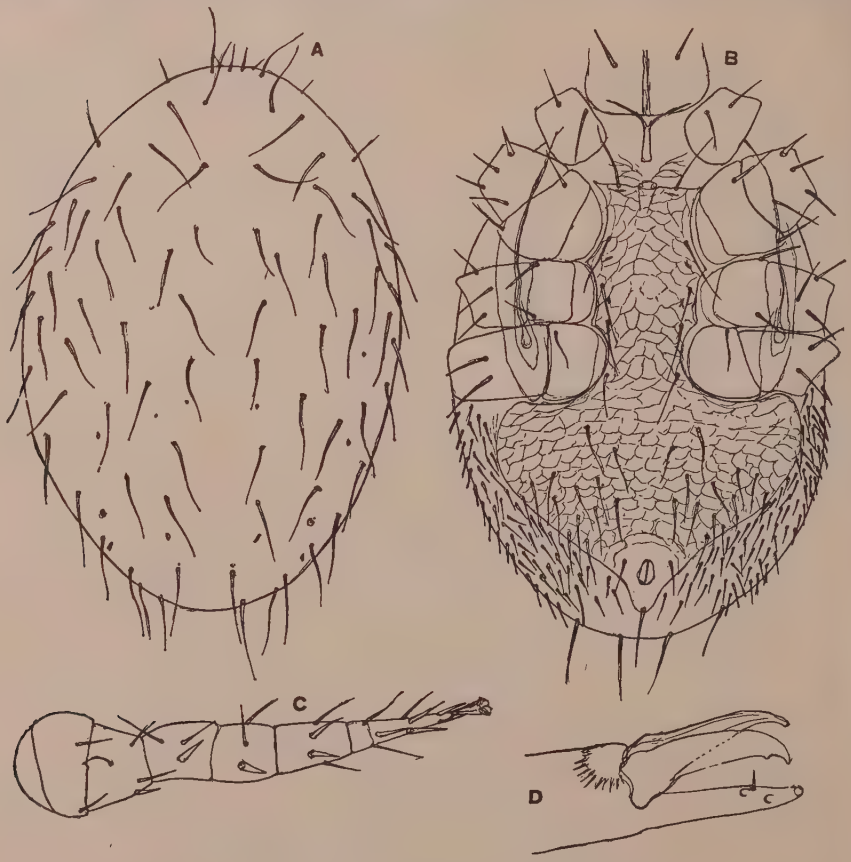


Fig. 4.—*Laelapsella humi*, gen. et sp. nov.
Male: *A*, dorsum; *B*, venter; *C*, leg II; *D*, chelicerae.

margin not quite reaching anal shield; anal shield triangular with the usual 3 setae; behind coxae IV a pair of short elongate lenticular metapodal shields; peritremal shields extending shortly behind stigma; on cuticle surrounding ventral shields 10 pairs of setae 32 μ long. Chelicerae are moderately long and slender, each finger with 2 small indistinct teeth and

fixed finger with simple seta (pilus dentarius), pulvillum fringed. Legs: slender and fairly short, II being a little stouter than others, I 455 μ long, II and III 350 μ, IV 416 μ; tarsi with caruncles and claws; all coxae without strong spines; femur and genu of leg II with 1 dorsal spine stronger than the rest, tibia with 2 such spines.

Male Allotype

Shape as in female. Length of idiosoma 949 μ, width 637 μ. Dorsal shield entirely covering dorsum, lightly reticulate, with c. 38 pairs of simple long setae to 104 μ. Venter: holoventral shield widely expanded behind coxae IV, with sides of ventri-anal portion rounded, and then lightly concave lateral of anus, with 4 pairs of sternal, 1 pair of genital and then 13 pairs of setae to 91 μ long, besides the 3 anal setae; surface lightly reticulate; laterally of ventri-anal with numerous short setae to 78 μ long. Chelicerae: fixed finger with 2 teeth and short seta; movable finger with 1 tooth and a spermatophore carrier as figured, not longer than the finger.

Locality and Host

Numerous specimens of both sexes from nesting material in burrows of mutton bird, *Puffinus tenuirostris*, from Fisher I., Bass Strait, Australia Jan. 1953, R. Mykytowycz. Another female from *Casuarina* debris from Sutherland, New South Wales (April 1949, coll. Clarke).

Remarks

These mites are possibly not truly parasitic, but may be scavengers in the debris of the nests.

Type female and male, and 6 female paratypes and 9 male paratypes in the collection of the South Australian Museum.

Genus GYMNOLAELAPS Berlese

Berlese, A., 1916, Redia 12: 170.

Type species *Laelaps myrmecophilus* Berlese 1892.

GYMNOLAELAPS ANNECTANS, sp. nov.

Fig. 5*A-E*

Female Holotype

Moderately sized, oval, lightly chitinized. Length of idiosoma 559 μ, width 351 μ. Dorsal shield covering entire dorsum except for a narrow band from shoulders backwards, with 37 pairs of simple tapering setae to 70 μ long, faintly reticulate. Venter: no pre-endopodal shields or jugular shields, but between base of tritosternum and sternal shield with a few transverse lines; sternal shield lightly reticulate, with 3 pairs of setae 52 μ long and 2 pairs of pores, anterior margin almost straight, posterior margin also almost straight and at about level of middle of coxae III, length of shield 170 μ; metasternal shields only represented by seta and pore; genitoventral shield flask-like, moderately expanded behind coxae

IV, 170 μ wide, reticulate, reaching anterior margin of anal, and posteriorly truncate, with 4 pairs of setae 58 μ long; anal shield triangular with 3 setae, the postanal longer than the adanals; a fairly large and 2

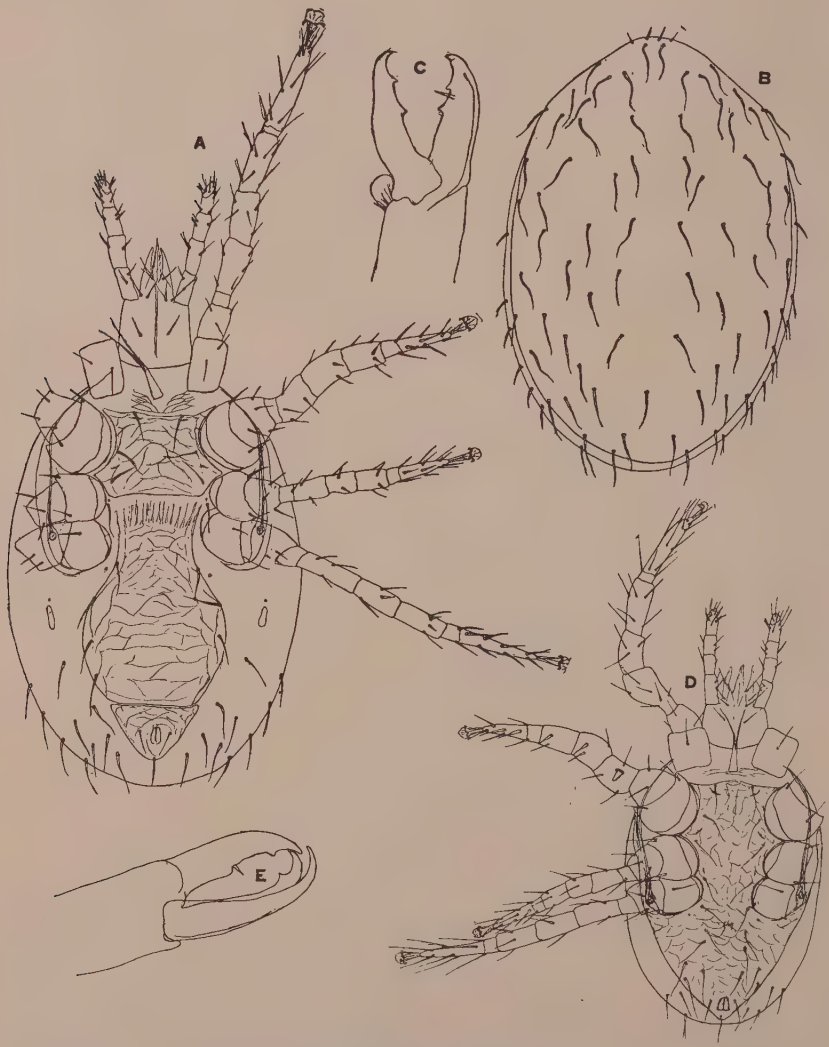


Fig. 5.—*Gymnolaelaps annectans*, sp. nov.
A-C, female: *A*, ventral view; *B*, dorsum; *C*, chelicerae; *D-E*, male: *D*, ventral view; *E*, chelicerae.

minute metapodal shields; on cuticle 10 setae on each side. Peritreme elongate, with stigma between coxae III and IV, peritremal shield

partially encircling coxae IV. Chelicerae as figured, each finger with 2 teeth. Specialized seta on palpal tarsus with 2 tines. Legs: fairly slender; leg I 480 μ long, II 390 μ, III 350 μ, IV 494 μ, all coxae unarmed; tarsi with caruncle and paired claws.

Male Allotype

As in female but smaller, length of idiosoma 390 μ, width 273 μ. All ventral shields united, expanded behind coxae IV to 208 μ wide; sternogenital portion with 5 pairs of setae and ventri-anal with 5 pairs of setae 39 μ long, in addition to the 3 anal setae. Coxae unarmed, femur of leg II with a short strong conical ventral spine. Leg I 403 μ long, II 325 μ, III 286 μ, IV 390 μ. Chelicerae are as figured, movable finger with only a single tooth and a strong curved spermatophore carrier slightly longer than the finger; fixed finger with 1 tooth and a short seta.

Locality and Host

The holotype and 16 paratype females and the allotype male and 8 paratype males from the nesting material in burrows of the mutton bird, *Puffinus tenuirostris*, from Fisher I., Bass Strait, Australia, January 1953 (R. Mykytowycz), in the collection of the South Australian Museum.

Remarks

In the setation of the dorsum and the legs this species appears to be distinct from any known species.

A further series of females has been received from Dr. E. H. Derrick of the Queensland Institute of Medical Research, collected from *Rattus rattus* (L.), at Taringa, Queensland (Aug. 1953).

Genus HAEMOLAELAPS Berlese

Haemolaelaps Berlese, 1910, Acari nuovi Redia 6: 261.

Type species *Laelaps* (*H.*) *marsupialis* Berlese 1910.

Atricholaelaps Ewing, 1929, "A Manual of External Parasites." p. 186.

Type *Laelaps reithrodontis* Ewing 1925.

Ischnolaelaps Fonseca, 1935-36, Mem. Inst. Butantan 10: 19.

Type *Ischnolaelaps reticulatus* Fonseca 1936.

HAEMOLAELAPS GLASGOWI (Ewing)

Fig. 6*A-C*

Laelaps glasgowi Ewing, 1925, Proc. Ent. Soc. Wash. 27: 6.
Laelaps californicus Ewing, 1925, Proc. Ent. Soc. Wash. 27: 5.
Laelaps virginianus Ewing, 1925, Proc. Ent. Soc. Wash. 27: 9.
?*Hypoaspis cricetophilus* Vitzthum, 1930, Zool. Jb. 60: 417.
Laelaps stegemani Hefley, 1936, J. Kans. Ent. Soc. 8: 22.
Haemolaelaps scalopi Keegan, 1946, Trans. Amer. Micr. Soc. 65: 71.
Atricholaelaps sigmodoni Strandtmann, 1946, J. Parasit. 32: 164.
?*Atricholaelaps strandtmanni* Fox, 1946, J. Parasit. 32: 598.
Haemolaelaps glasgowi Strandtmann, 1949, J. Parasit. 35: 325-52.

The generic status and synonymy of *Haemolaelaps* and the specific synonymy of *glasgowi* Ewing have been very fully discussed by Professor

R. W. Strandtmann 1949 (loc. cit.). The species is widespread in most States of North America, and it has been intercepted in shipments to the United States of America from Cuba, Mexico, and Guatemala, while *H. cricetophilus* Vitz. was described from China.

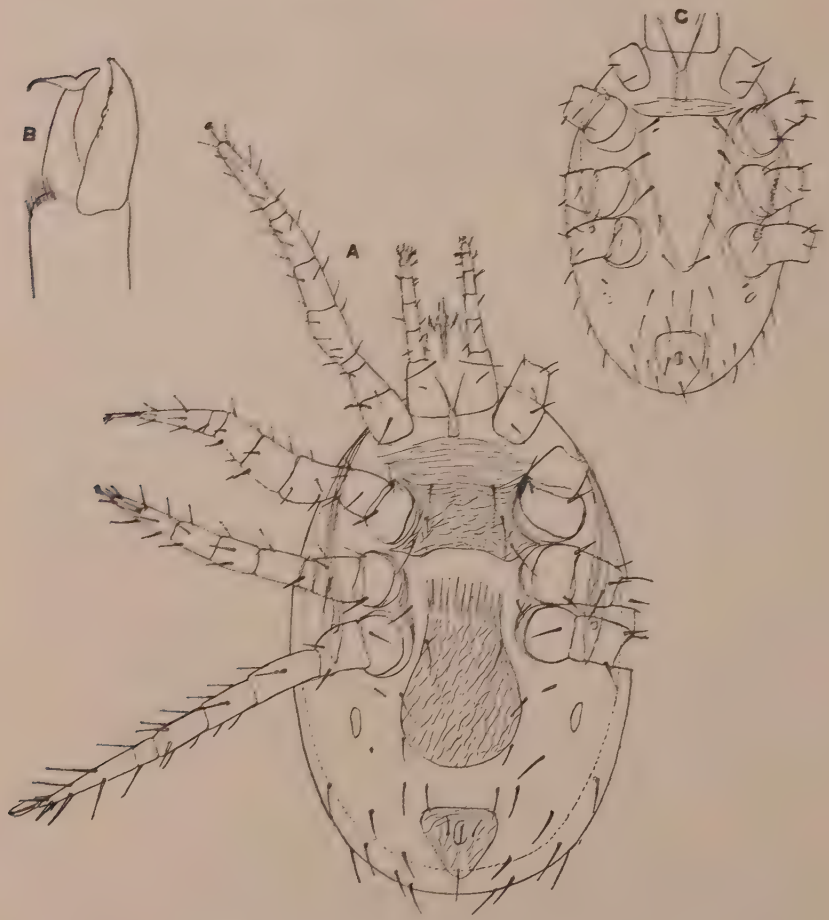


Fig. 6.—*Haemolaelaps glasgowi* (Ewing).
A-B, female: *A*, ventral view; *B*, chelicerae; *C*, nymphal venter.

Strandtmann 1945 (loc. cit., p. 349) lists the known hosts of this mite, which include seven species of birds, and no fewer than 75 species of mammals.

The following new records both for host and localities can now be given for this species as follows:

(i) A single female from nesting material of mutton birds, *Puffinus tenuirostris*, from Fisher I., Bass Strait, Australia (Jan. 1953, R. Mykytowycz).

(ii) Many specimens from the Fairy Penguin, *Eudyptula minor* (Forster), from Greenly I., South Australia, (16.xii.1948, F. J. Mitchell), and from the same host, from Ravine de Casuars, Kangaroo I., South Australia (18.x.1951, G. F. Gross).

Haemolaelaps marsupialis Berlese

Fig. 7*A-E*

Redescription: *Female Holotype*

Lightly chitinized, broadly oval. Dorsal shield lightly reticulate, not entirely covering dorsum, with 13 pairs of short 39 μ setae on the disk and many long 90-117 μ setae on edge of shield and on lateral margins of dorsum. Length of idiosoma 910 μ, width 793 μ. Venter: tritosternum as figured with lateral ciliations on base; some light striations between tritosternum and sternal shield; sternal shield wider than long, with anterior and posterior margins lightly concave, with 3 pairs of setae 80 μ long, and 2 pairs of pores; metasternal shields only represented by seta and pore; genitoventral shield flask- or drop-shaped with fringed anterior and rounded posterior ends, moderately widely separated from anterior of anal shield, with 1 pair of setae; anal shield triangular with straight anterior margin and 3 setae; a long lenticular and 2 minute rounded metapodal shields; posterior of coxae IV with 15 pairs of setae to 80 μ long. Chelicerae with fingers of equal length, the movable finger with a single tooth, and the fixed with an apparent hyaline sheath and a long flagelliform seta; stigma situated between coxae III and IV. Legs: fairly slender, II the strongest; I 689 μ long, II 494 μ, III 480 μ, IV 728 μ, coxae and other segments without special armature, tarsi with caruncles and paired claws.

Male Allotype

As in female but smaller. Length of idiosoma 650 μ, width 455 μ. All ventral shields fused and expanded behind coxae IV to 299 μ wide; sternogenital portion with 5 pairs of setae, ventri-anal with 4 pairs of setae. Legs: I 572 μ long, II 494 μ, III 494 μ, IV 689 μ; coxae unarmed. Chelicera with fixed finger only about half length of movable finger and with a long flagellum-like seta, movable finger with 1 tooth and a simple spermatophore carrier of its own length.

Locality and Host

Thirty-one females, allotype and 7 paratype males from nesting material from burrows of *Puffinus tenuirostris* from Fisher I., Bass Strait, Australian (Jan. 1953, R. Mykytowycz), in the collection of the South Australian Museum.

Remarks

This species which is the type of the genus was briefly described by Berlese without any figures. Its status has been uncertain since its

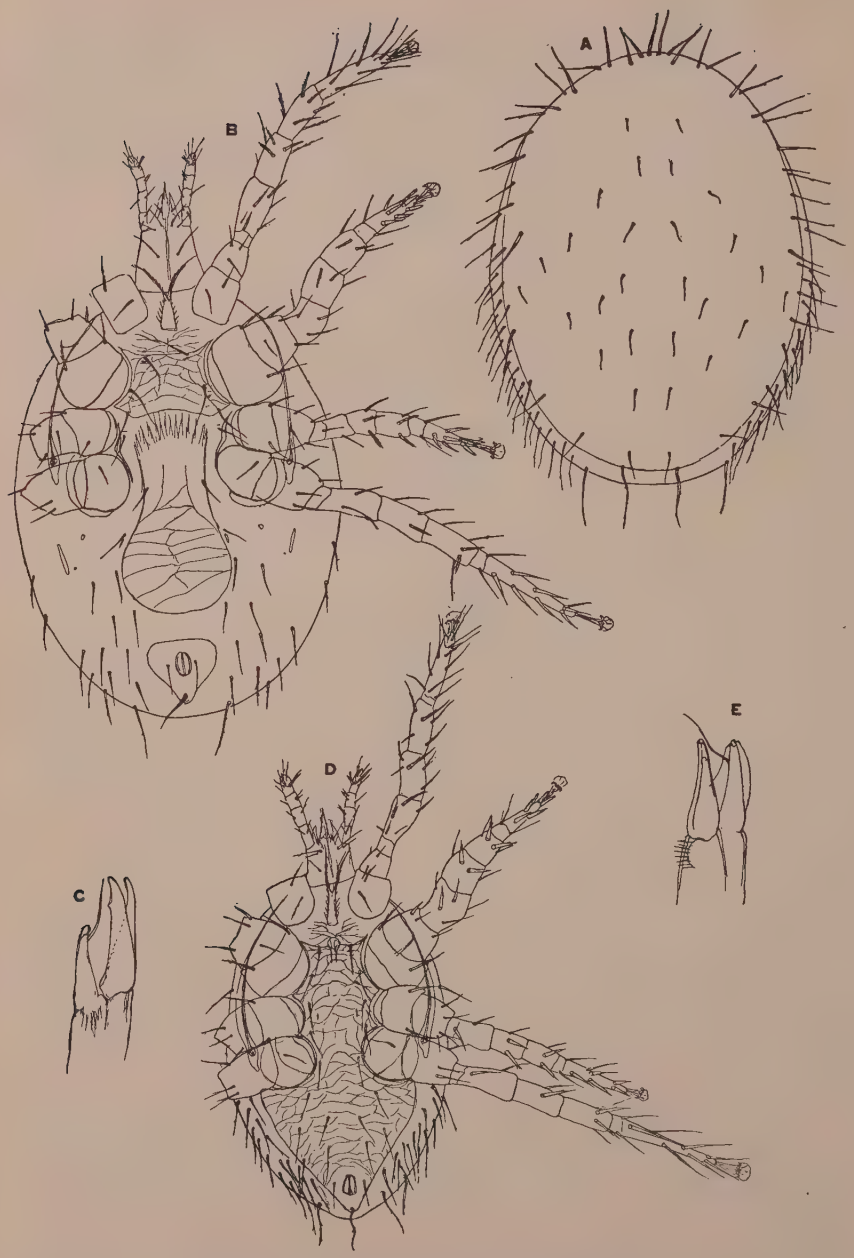


Fig. 7.—*Haemolaelaps marsupialis* Berlese 1910.
A, *B*, *E*, female: *A*, dorsum; *B*, ventral view; *E*, chelicerae. *C*, *D*, male: *C*, chelicerae; *D*, ventral view.

description, owing to the inaccessibility of the type material. I have, however, recently been greatly indebted to Dr. G. Owen Evans of the British Museum (Nat. Hist.) for tracings of drawings of the type specimens made by him during a recent visit to Florence. Although the material is stated to be in poor preservation, the drawings clearly show that the material from the mutton bird burrows, as well as specimens in the South Australian Museum and the Queensland Institute of Medical Research from bandicoots from various localities in Queensland, are identical with *marsupialis*.

As with other members of the genus this species is most probably a blood sucker.

Genus MESOLAELAPS Hirst

Hirst, S., 1926, Proc. Zool. Soc. Lond., Pt. 3: 800.

Type species *Mesolaelaps anomalus* Hirst 1926.

MESOLAELAPS AUSTRALIENSIS Hirst

Fig. 8*A-E*

Laelaps (*Mesolaelaps*) *australiensis* Hirst, 1926, Proc. Zool. Soc. Lond., Pt.. 3: 840 (fig. 11).

Mesolaelaps australiensis, Womersley, 1937, Parasitology 29 (4): 538.

This species was originally described from mice from Toowoomba, Qld, but only from the female sex. Womersley in 1937 recorded it from rats from Sydney, N.S.W., on Hirst's identification, and from *Rattus lutreola* Gray, from Lake Alexandrina, S. Aust., May 1936, from *Perameles gunni* Gray, from between Hamilton and Portland, Vict., 1936 and from *Perameles macrura* Gould, from the Ingham district, Qld, without date.

A considerable number of both sexes were obtained from the nesting material of the mutton bird, *Puffinus tenuirostris*, on Fisher I., Bass Strait, Australia (Jan. 1953, R. Mykytowycz); the male is here described and figured for the first time.

Male Allotype

Shape as in female, lightly chitinized. Length of idiosoma 676 μ, width 455 μ. Dorsal shield, almost covering the whole of dorsum, with long slender setae, 117 μ long, the posterior ones of which are shortly ciliated, *c.* 25 pairs; setae on lateral part of dorsum shorter, to 65 μ. Venter: all shields united, the holoventral shield expanded behind coxae IV to 325 μ; 1st pair of sternal setae 45 μ long and ciliated, remaining setae on holoventral to 90 μ long and simple; on the ventri-anal portion *c.* 22 pairs of setae besides the 3 anal setae; outside of the ventri-anal with numerous long setae, the posterior the longest and ciliated. Legs: I 650 μ long, II 520 μ, III 585 μ, IV 910 μ; all slender; no special armature on coxae; leg spines, especially the longer ones are ciliated; tarsi with long caruncle and paired claws. Chelicerae are as figured, the fixed finger with 1 tooth

and a seta (pilus dentarius), movable finger with 1 tooth and a strong spermatophore carrier, which is slightly longer than the finger and curves around it apically.

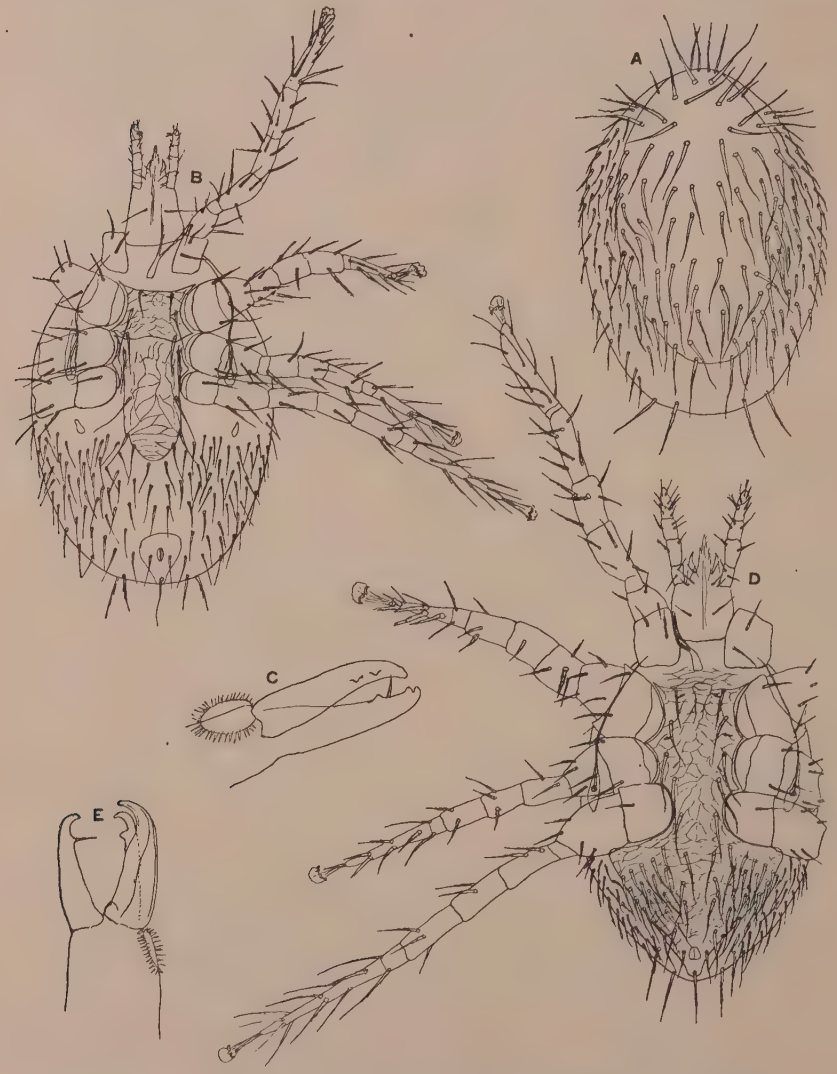


Fig. 8.—*Mesolaelaps australiensis* Hirst.
A-C, female: *A*, dorsum; *B*, ventral view; *C*, chelicerae. *D*, *E*, male: *D*, ventral view; *E*, chelicerae.

Remarks

The allotype and 11 paratype males are in the collection of the South Australian Museum.

Superfamily **UROPODINA** Kramer 1881
Family ?**PHAULODINYCHIDAE** Berlese

Berlese, A., 1917, Redia 12 (1).

Despite the recent attempts of Trägärdh and other workers to disentangle the classification of the Uropodina the following new genus can be referred only tentatively to the Phaulodinychidae.

Genus AUSTRUROPODA, gen. nov.

Tritosternum exposed between coxae I. Leg grooves well developed. Dorsal shield entire, smooth, separated except on posterior 4th and anteriorly from lateral shields. Stigmata between coxae II and III. A row of 3-4 branched setae on each side behind coxae IV.

Type species *Austruropoda tasmanica*, sp. nov.

AUSTRUROPODA TASMANICA, sp. nov.

Fig. 9*A-I*

Female Holotype (Fig. 9*A-F*)

Dark brown, strongly chitinized. Shape is ovoid with strongly pronounced shoulders and conical snout. Length of idiosoma 780 μ, width 520 μ. Legs fairly stout, all shorter than body with long slender caruncle and paired claws; I 429 μ long, II and III 330 μ, IV 416 μ. Dorsal shield entire, smooth, lightly united anteriorly near shoulders with the lateral shields, which extend well backwards where they again touch the dorsal shield; dorsal shield with the numerous stiff setae which posteriorly tend to be lightly ciliated to 50 μ long, lateral shields with similar setae. Venter: tritosternum with short basal trunk below coxae I, with long 3-branched lacinia; genital shield elliptical with straight posterior edge, without setae, extending from front of coxae II to just beyond front of coxae IV; sternal-metasternal shield fused with ventri-anal, with 6 pairs of short setae and 5 pairs of pores as figured; just behind coxae IV on each side is a transverse row of 3-4 strong branched, or ciliated, setae; behind the latter, on the ventri-anal shield are 5 pairs of strong setae to 50 μ long; the leg grooves are large and well developed, and in those of leg III lie the stigmata; with irregularly curved peritreme; coxae and trochanter of leg I have rather poorly developed laminae as figured. Chelicerae are as figured, the fixed finger with a short stout hyaline appendage.

Male Allotype

General facies, size, and dimensions as in female. Venter: genital orifice situated between coxae III with setae as figured, the setae on each side and posterior of genital opening rather longer than in female. Chelicerae as described in female.

Locality and Host

A large number of specimens of both sexes from the debris in the nests of the mutton birds, *Puffinus tenuirostris,* from Fisher I., Bass Strait, Australia (Jan. 1953, R. Mykytowycz).

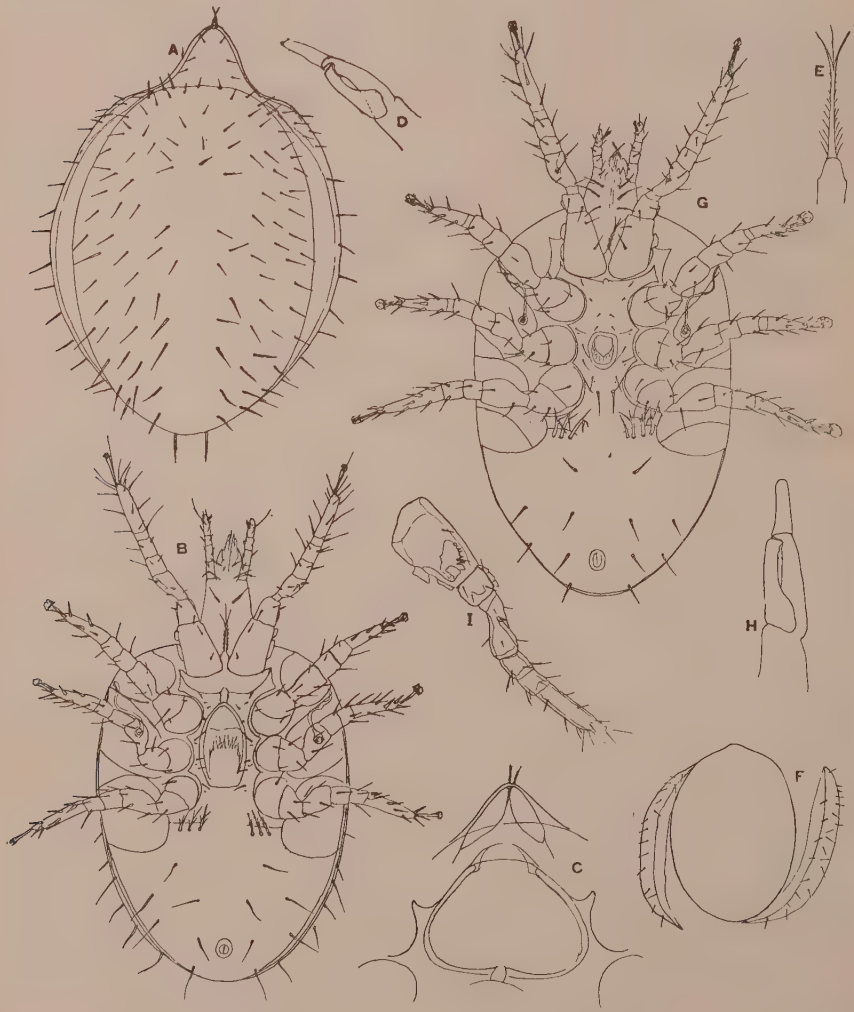


Fig. 9.—*Austruropoda tasmanica,* gen. et sp. nov.
A-F, female: *A,* dorsum; *B,* ventral view; *C,* camerostome; *D,* chelicerae; *E,* tritosternum; *F,* dorsal and lateral shields; *G-I,* male: *G,* ventral view; *H,* chelicerae; *I,* leg I.

Remarks

Holotype female and allotype male and paratypes in the collection of the South Australian Museum.

Suborder **TROMBIDIFORMES** Reuter 1909
Superfamily **TARSONEMINI** Canestrini & Fanzago 1877
Family **SCUTACARIDAE** Oudemans

Oudemans, A. C., 1916, Acarol. Aanteekeningen. LXI. Ent. Ber. Amst. IV: 92.

Genus VARIATIPES Paoli

Paoli, G., 1911, Redia 7: 222.

Type species *Disparipes nudus* Berlese 1886.

VARIATIPES LONGISETOSUS, sp. nov.
Fig. 10*A-B*

Adult Holotype

Sex? Length 325 μ, width 247 μ. Gnathosoma and apical portions of legs I and II projecting in front of the large overlapping anterior dorsal

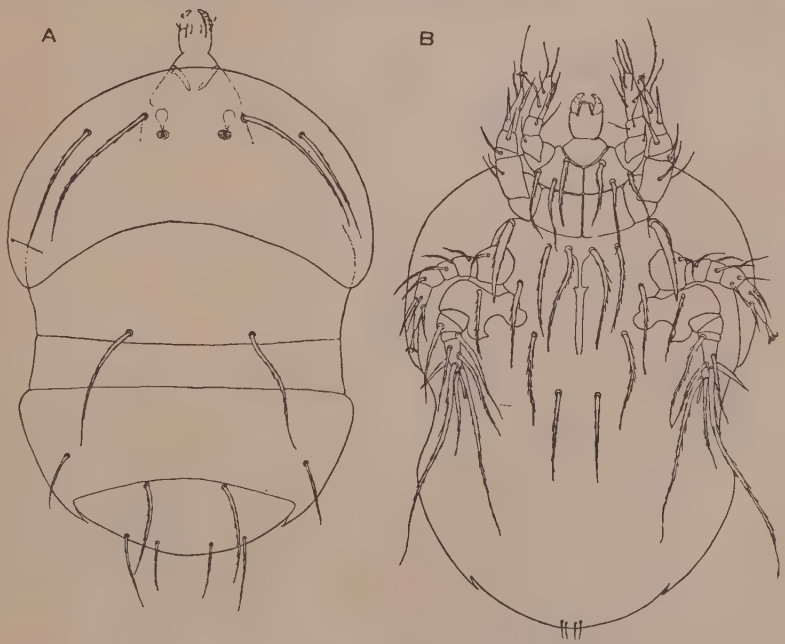


Fig. 10.—*Variatipes longisetosus*, sp. nov.
A, dorsum; *B*, ventral view.

shield. Anterior dorsal shield or segment the widest, with 2 pairs of long anterior setae, the inner pair the longer to 120 μ, the outer to 84 μ; next segment dorsally together with the next again forming a slight constriction or waist; the 2nd segment carries 1 pair of setae to 102 μ long; the 4th dorsal plate or segment is wider with rounded anterior corners and has 1 pair of sublateral setae to 48 μ long; the remaining dorsal shield or shields have a pair of long 67.5 μ anterior submedial setae, and 2 pairs of posterior setae to 48 μ long; all these dorsal setae are strongly ciliated. Lying

beneath the dorsal shield anteriorly, but still dorsal to the covered portion of the body is the usual pair of clavate sensillae. Ventrally, the species is as figured with small paired claws only on legs II and III; leg IV with only 4 free segments and terminating in long ciliated setae; the "external posterosternal setae" of Paoli are situated well in front of the interior posterosternal setae.

Locality and Host

Numerous specimens from amongst the debris of mutton bird nests from Fisher I., Bass Strait, Australia (Jan. 1953, R. Mykytowycz).

Remarks

In the position of the posterior sternal setae this species is closely related to *V. nudus* Berlese and *V. montanus* Paoli. It differs markedly from these as from all other species of which I am aware, in the very long and ciliated dorsal and ventral setae, and in the gnathosoma not being covered by the anterior dorsal shield.

The type and paratypes in the South Australian Museum.

Family **TARSONEMIDAE** Kramer

Kramer, P., 1877, Arch. Naturgesch. 43 (1): 215-47.

Genus TARSONEMUS Canestrini & Fanzago

Canestrini, G. & Fanzago, 1876, Atti Soc. Padua 5 (1): 14.

Type species *Chironemus minusculus* G. Canestrini & Fanzago 1876.

TARSONEMUS, sp. nov., cf. CONFUSUS Ewing

Fig. 11*A-D*

Many females of a species of *Tarsonemus* from mutton bird nests from Fisher I., January 1953 (R. Mykytowycz), agree with Ewing's species according to his key to the females, and on his description and figure of the 4th leg of the female. Unfortunately no males were found amongst a large number of females, hence there is a possible question as to whether the species is really *confusus*. The type material came from *Delphinium belladonna* from Maryland, U.S.A., and Ewing also recorded it from many other plants from a number of other States of the United States of America. As far as I know it has not been found elsewhere.

The present specimens, however, are considerably smaller than *confusus* for which Ewing gives the length of the female 194 μ and the width 133 μ. In size and general resemblance our specimens agree also with *T. minimax* Vitzthum 1926 described as associated with *Ips curvidens* Germar, from Thaya, Lower Austria. Unfortunately, Vitzthum does not refer in detail to the sensory seta of tarsus I in the way that Ewing in his 1939 paper does. Also Vitzthum's figure of the ventral surface of the female does not show a basal seta at all on the femoral segment of the 4th leg.

Our material may be characterized by the following description of a female deposited, with other specimens in the South Australian Museum.

Female

Colour light yellowish. Shape broadly oval but the sides medially rather straight. Length of idiosoma 132 μ, width 84 μ. Capitulum (gnathosoma) 28 μ long by 20 μ wide. Chelicerae and palpi are small and not clearly seen, as figured. Dorsum as figured, propodosoma with 4 pairs

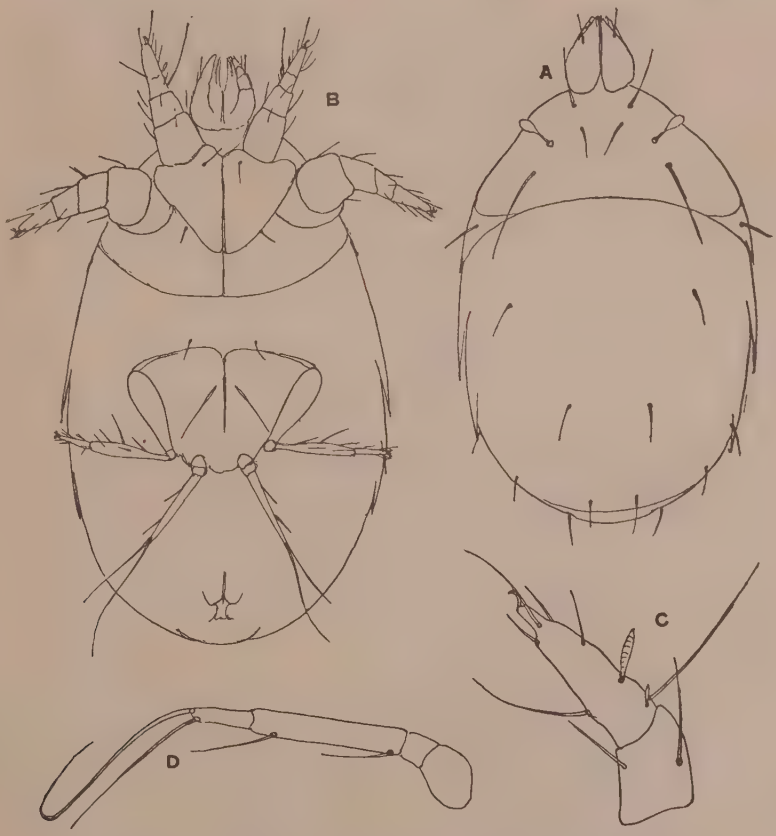


Fig. 11.—*Tarsonemus*, sp. nov., cf. *confusus* Ewing.
Female: *A*, dorsum: *B*, ventral view; *C*, tarsus I; *D*, leg IV.

of simple setae besides the pair of clavate sensillae, the pair of setae immediately behind sensillae the longest to 28 μ, remainder of dorsum with 6 pairs of setae. Legs: tarsi I with a single claw about twice as long as tibia, with the distal sensory club at about two-fifths from the base, basal sensory club only about half the length of distal and slightly basal of the base of the 1st seta which is 24 μ long, tarsi II and III with paired claws, II with 1 sensory club; legs I and II much stronger and thicker than III and IV; coxae I and II each with a fine short seta, epimera of coxae I not uniting medially; epimera of III and IV also not distinctly

conjoined medially; leg IV not over-reaching margins of body, as figured; 3rd segment slightly longer than rest taken together, with the basal seta at least half as long as the distal seta, 4th segment about one-third length of 3rd, with the subapical seta more than twice (almost thrice) as long as segment, the apical seta very long 35 μ, about equal to or longer than entire leg.

Suborder **SARCOPTIFORMES** Reuter 1909

Superfamily **ACARIDIAE** Latreille 1802

Family **ACARIDAE** Ewing & Nesbitt

(= **TYROGLYPHIDAE** Donnadieu 1868, et auct.)

Ewing, H. E., & Nesbitt, H. H. J., Proc. Biol. Soc. Wash. 55: 121-4.

Subfamily **RHYZOGLYPHINAE** Zachvatkin

Zachvatkin, A. A., 1940, Uch. Zap. Mosk. Godeidarst Univ. No. 42, 2 Vols. pp. 7-68.

Genus ACOTYLEDON Oudemans

Acotyledon Oudemans, A. C., 1903, Ent. Ber. Amst. 1: 11.

Type species *Acotyledon paradoxa* Oudemans 1903.

Eberhardia Oudemans, A. C., 1924, Ent. Ber. 6: 135, 230.

Type species *Tyroglyphus michaeli* Oudemans 1924.

Subgenus COSMOGLYPHUS Oudemans

Oudemans, A. C., 1932, Ent. Ber. Amst. 8: 183, 308.

Type species *Tyroglyphus krameri* Berl. 1881.

ACOTYLEDON (COSMOGLYPHUS) MYKYTOWYCZI, sp. nov.

Fig. 12*A-F*

Female Holotype

Shape elongate oval. Length of idiosoma (non-gravid) 350 μ, (gravid) 520 μ; width 220 μ, 325 μ. Gnathosoma clearly seen from above, 90 μ long, mandible stoutly chelate 98 μ long. The propodosomatal shield is longer than wide with the posterior edge just in front of the scapular setae and somewhat rounded, lateral margins slightly indented medially. Dorsal setae mostly long, slender, and sparsely ciliated in distal part, arranged as follows: vertical internals, *V.i.*, on the apical edge of propodosoma, to 70 μ long; vertical externals, *V.e.*, minute, in the indentation of the shield; Grandjean's organ and "Nuchal" seta 36 μ long, and only indistinctly barbed; internal scapular, *Sc.i.*, to 70 μ long and 40 μ apart, external scapular, *Sc.e.*, placed 23 μ from the nearest *Sc.i.* and to 170 μ long; the 2 median longitudinal rows of 4 dorsal setae, D_1 40 μ, D_2 112 μ, D_3 126 μ, D_4 154 μ; lateral rows of 2 setae, L_1 75 μ, L_2 112 μ; internal posterior setae, *P.i.*, 140 μ, external posterior, *P.e.*, 84 μ; humeral setae, *H.i.*, 64 μ, *H.e.*, 112 μ (and on venter, *H.v.*, 28 μ). Venter: on the anterior part in front of coxae I laterally on each side is a short, shortly ciliated seta 20 μ long; coxae in 2 pairs, epimera I united in medial line, coxae I and III with a

short 20 μ seta; genitalia placed between coxae IV and flanked by a pair of short setae. Anal opening elongate, subterminal, flanked on each side by 2 setae and at the apex by another seta corresponding to the postanal setae of the male. Legs: shorter than body, I 234 μ, II 234 μ, III 234 μ,

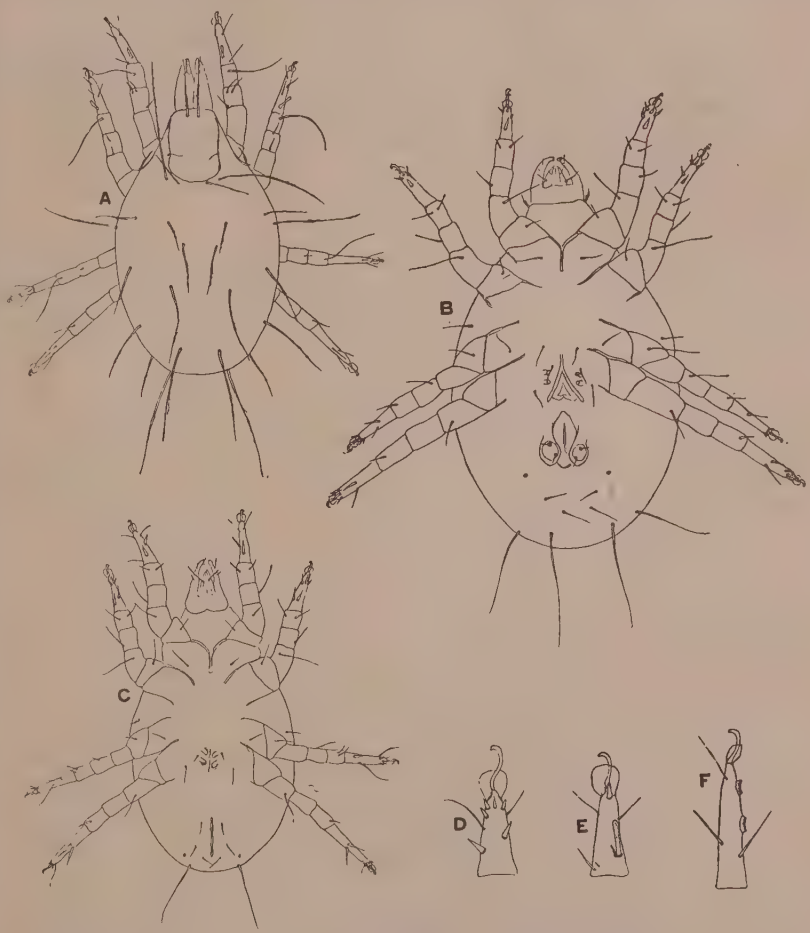


Fig. 12.—*Acotyledon* (*Cosmoglyphus*) *mykytowyczi*, sp. nov.
A, dorsal view of female; *B*, ventral view of male; *C*, ventral view of female; *D*, tarsus I of male; *E*, tarsus I of female; *F*, tarsus IV of male.

IV 260 μ; tarsi I about as long as tibia plus genu; inner and outer apical setae on genu I about equal in length; tarsi I with sensory club with slightly expanded apex and a short spine at its base, ending in a strong claw whose base is enveloped in the pulvillus, at the base of the claw with 3 ventral and 1 dorsal spine.

Male Allotype

Shape as in female. Length of idiosoma 480 μ, width 325 μ. Dorsal setae arranged as in female; *V.i.* 70 μ, *V.e.* 16 μ, Grandjean's organ and seta 42 μ and 40 μ long respectively; *Sc.i.* 75 μ, *Sc.e.* 174 μ, *Sc.i.* 36 μ apart and 28 μ from *Sc.e.*; D_1 56 μ, D_2 100 μ, D_3 168 μ, D_4 188 μ; L_1 98 μ, L_2 145 μ; *P.i.* 134 μ, *P.e.* 98 μ; *H.i.* 75 μ, *H.e.* 148 μ (and on venter) *H.v.* 10 μ, *P.v.* 154 μ, and postanal interior, *Pa.i.* 64 μ, *Pa.e.* 33 μ. Genital organ situated between coxae IV; anal slit flanked by sucking disks as figured. Legs: I 260 μ long, II 260 μ, III 286 μ, IV 325 μ; disks on tarsi IV 20 μ apart 34 μ from base and 28 μ from apex; tarsus apically with 3 ventral short stout spines and 1 dorsal.

Locality and Host

The holotype male and allotype female and a number of paratypes of both sexes from the nesting material of the burrows of the mutton bird, *Puffinus tenuirostris*, from Fisher I., Bass Strait, Australia (Jan. 1953, coll. R. Mykytowycz), in the collection of the South Australian Museum.

Remarks

In Zachvatkin's key to the species of *Acotyledon* this new species will come close to *A. batsylevi* Zach. from U.S.S.R. The slender dorsal setae will place both these species in the subgenus *Cosmoglyphus* Ouds. *A. mykytowyczi* differs from *batsylevi* in that D_3 and D_4 have a much greater ratio of length to body length, at least 35 per cent. as compared with 22 per cent. given for *batsylevi*.

The new species is dedicated to Dr. R. Mykytowycz, who obtained the nesting material.

Genus THYREOPHAGUS Rondani
(= MONIEZIELLA Berlese 1897)

Rondani, 1874, Bull. Soc. ent. ital. 6: 67.

Type species *Acarus entomophagus* Laboulbene 1852.

Thyreophagus corticalis (Michael)
Fig. 13*A-C*

Tyroglyphus corticalis Michael, A. C., 1885, J. R. Micr. Soc. (11): 27-31, pl. III, fig. 1-14.

Histiogaster entomophagus Kramer, 1899 (in pt.), Bronn's Tierreich Lfg. 7: 142.

Histiogaster corticalis, Berlese, 1890, Acari Myriopoda et Scorpiones Italia Reperta fasc. 57: No. 7; Michael, 1903, Brit. Tyroglyp, ii: 66; Vitzthum, 1929, Tierwelt. Mitteleuropas, iii: 70.

Monieziella mali Berlese, 1897, Acari, Myriopoda, et Scorpiones, Crypt.: 107.

Thyreophagus corticalis, Womersley, 1941, Rec. S. Aust. Mus. 6 (4): 459, fig. 4 *A-D*.

This cosmopolitan species was found in moderate numbers amongst the debris in the burrows of mutton birds on Fisher I., Bass Strait, Australia (Jan. 1953, R. Mykytowycz).

Subfamily **ACARINAE** Nesbitt

Nesbitt, H. H. J., 1945, Canad. J. Research, D. 23: 139-88.

Genus TYROPHAGUS Oudemans

Oudemans, A. C., 1924, Entom. Ber. 6: 136, 250.

Type species *Acarus putrescentiae* Schrank 1781.

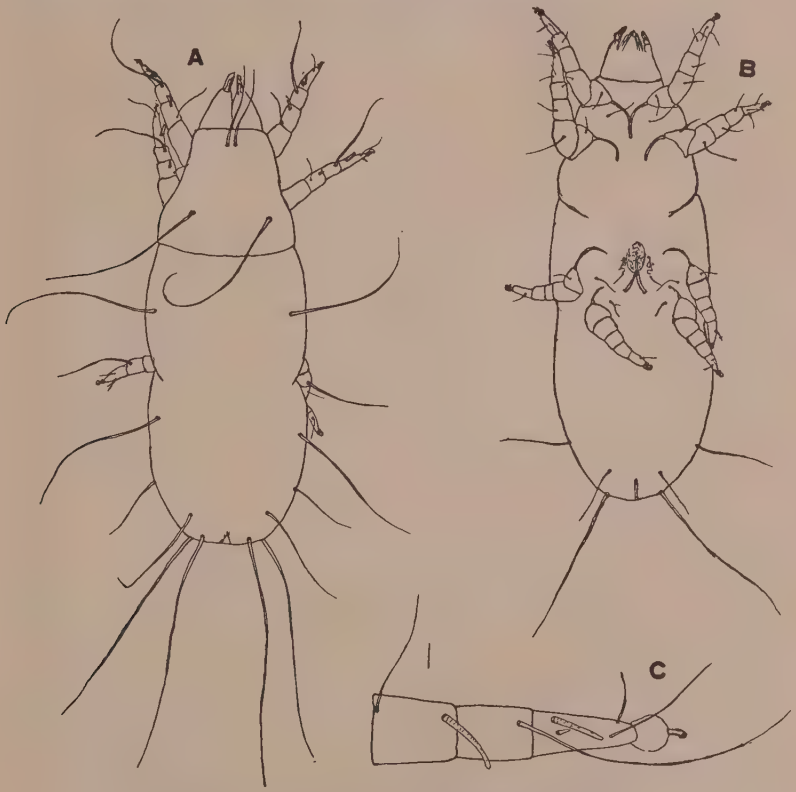


Fig. 13.—*Thyreophagus corticalis* (Michael).
Female: *A*, dorsal view; *B*, ventral view; *C*, leg I.

TYROPHAGUS CASTELLANII Hirst 1912

Fig. 14*A-E*

Tyrophagus longior var. *castellanii* Hirst.
Tyrophagus noxius Zachvatkin 1941.

Amongst the nesting material from mutton bird, *Puffinus tenuirostris*, burrows on Fisher I., Bass Strait, Australia (Jan. 1953) were a few specimens of both sexes of this common and widely distributed species. It is essentially a detricolous species and in no way parasitic. I have specimens from many parts of Australia, from soya beans from Adelaide, S. Aust., from cultures of cockroaches, from the Institute for Medical Research, Brisbane, and from a house at Cairns, Queensland.

It is close to *T. tenuiclavus* Zach. which also occurs in Australia. In the latter species setae D_2 are short and the tarsal suckers of the male are more basad.

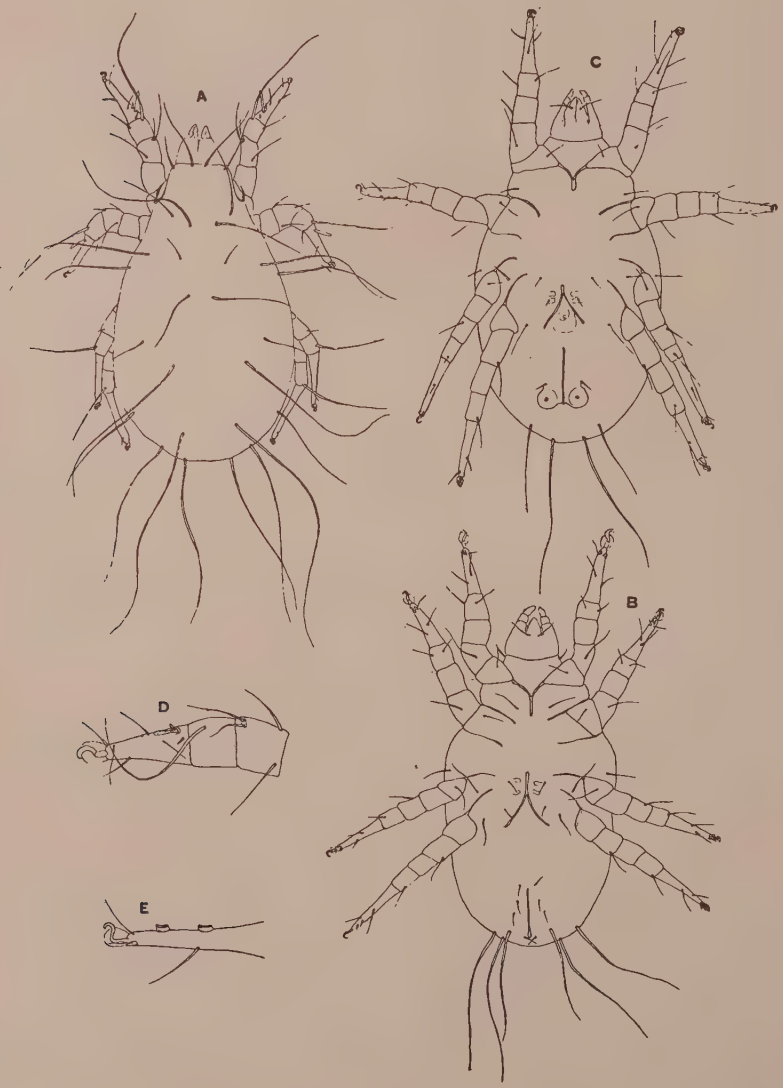


Fig. 14.—*Tyrophagus castellanii* Hirst.
A, dorsal view of female; *B*, ventral view of female; *C*, ventral view of male; *D*, leg I of female; *E*, tarsus IV of male.

Family **ANALGESIDAE** Megnin & Trouessart

Megnin & Trouessart, 1883, C.R. Acad. Sci. Paris 97.

Subfamily **PTERONYSSINAE** V. B. Dubinin 1953

Genus ZACHVATKINIA V. B. Dubinin

Dubinin, V. B., 1949, The fauna of the feather mites occurring on birds belonging to the order Procellariiformes and its peculiarities. Mag. Parasit. Moscow (in Russian). (= *Giebelia* Trouessart, 1915, preoc., *Pseudogiebelia* Radford 1950).

Type species *Dermaleichus puffini* Buchholz.

Fig. 15.—*Zachvatkinia*, sp. nov., cf. *puffini* (Buchholz).
A, dorsal view of female; *B*, ventral view of female; *C*, dorsal view of male; *D*, ventral view of male; *E*, dorsal view of nymph; *F*, ventral view of nymph.

ZACHVATKINIA, sp. nov., cf. PUFFINI (Buchholz)

Fig. 15*A-F*

Dermaleichus puffini Buchholz, 1869, Bemerk. Art. Gatt. *Dermaleichus* 37: t. 4, fig. 23, 24.

Pteronyssus puffini Canestrini G., 1886, Prosp. Acarof. 2: 274, t. 21, fig. 1.

Pteronyssus sternae Canestrini G., 1879, Atti. Soc. Ven.-Trent. Padua 6: 38, t. 1, fig. 9.

Pteronyssus puffini Canestrini G. & Kramer F., 1899, Bronn's Tierreich, Lfg. 7: 84.

Giebelia puffini Bedford G. A. H., 1932, Eighteenth Report of the Director Vet. Serv. Anim. Ind., Pretoria.

Zatvatkinia puffini is recorded by Canestrini & Kramer 1899 from *Dromus ardeola* Payk. and many species of *Sterna, Larus, Puffinus, Procellaria,* etc. and said to be almost cosmopolitan. Bedford 1932 recorded it from *Dromus ardeola* and other birds but as his paper is but a check list it is not clear whether these are fresh records or only a repeat of Canestrini and Kramer.

A number of specimens of what seems to be this species were taken from the down of young mutton birds, *Puffinus tenuirostris,* on Fisher I., Bass Strait, Australia, by Dr. Mykytowycz in January 1953. Most of the recent literature on these mites is by V. B. Dubinin in various Russian publications and not available to me. However, I have recently received a copy of his work on the Feather mites (Analgesoidea) (Dubinin 1951).* In this he refers to several species of *Zachvatkinia,* and includes various figures of details of *sternae* Canestrini, *stercoraria* V. B. Dubinin, and *puffini* (Buchholz). Of *puffini* he only gives fig. 92 (1) of the male. From his figures our specimen appears to be Buchholz species; but for the sake of future Australian workers and to enable others better situated for literature to verify the identification I give complete figures of the Fisher I. material.

LIST OF GENERA AND SPECIES

* DUBININ, V. B. (1951).—Feather mites (Analgesoidea). I. An introduction to their study. *Fauna U.S.S.R.* 6: 5.

THE CLASSIFICATION AND DISTRIBUTION OF TABANIDAE (DIPTERA)

II. HISTORY: MORPHOLOGY: CLASSIFICATION: SUBFAMILY PANGONIINAE

By I. M. MACKERRAS*

(*Manuscript received March* 15, 1955)

CONTENTS

Summary

Classifications proposed in the past are reviewed, the male and female genitalia described in some detail, and the relationships which they indicate found to agree with those suggested by the known larvae and pupae. Parallel evidence from external characters of the adults is partly obscured by convergent evolution between the subfamilies.

Pelecorhynchus, Bequaertomyia, and *Heterostomus* are excluded from the Tabanidae. The genera of Pangoniinae are defined.

The following cannot be placed from descriptions: Palaearctic — *Scaptiella* End.; spp. described as *Corizoneura.* Nearctic — *Zophina* Philip. Neotropical — *Leptofidena* Kröb.

The suggested arrangement of the remaining genera is as follows, those placed tentatively from descriptions being indicated by an interrogation mark.

PANGONIINI

Palaearctic — *Pangonius* Latr., with possible subgenera *Pangonius* Latr., *Tanyglossa* Mg., and ?*Ectinocerella* Ség.

Nearctic — *Esenbeckia* Rond.; *Apatolestes* Will.; *Brennania* Philip; *Pilimas* Bren.; *Stonemyia* Bren.; *Asaphomyia* Stone.

* Queensland Institute of Medical Research, Brisbane.

Neotropical — *Esenbeckia* Rond.; *Proboscoides* Phil.; *Chaetopalpus* Phil.; *Protodasyapha* End.; ?*Histriosilvius* Kröb.; ?*Protosilvius* End.

Australasian — *Austroplex*, gen. nov. (type *goldfinchi*, sp. nov.); *Ectenopsis* Macq., with subgenera *Ectenopsis* Macq., *Leptonopsis*, subgen. nov. (type *vittata*, sp. nov.), *Parasilvius* Ferg., and *Paranopsis*, subgen. nov. (type *lutulentus* Hut.); *Caenoprosopon* Ric.; *Therevopangonia*, gen. nov. (type *insolita*, sp. nov.).

SCIONINI

Nearctic — *Goniops* Aldr.

Neotropical — *Mycteromyia* Phil.; *Pityocera* G.-T.; *Elaphella* Bezzi; *Scione* Walk.; *Fidena* Walk.; *Scaptia* Walk., with subgenera *Scaptia* Walk., *Pseudoscione* Lutz *et al.*, and *Pseudomelpia* End.

Ethiopian — *Scaptia* Walk., subgenus *Pseudoscione* only.*

Australasian — Australia: *Scaptia* Walk., with subgenera *Scaptia*, *Pseudoscione*, *Myioscaptia*, subgen. nov. (type *violacea* Macq.), *Plinthina* Walk., and *Palimmecomyia* Tayl. New Guinea: *Pseudoscione* only. New Zealand: *Pseudoscione* only.

PHILOLICHINI

Ethiopian — *Buplex* Aust.; *Ommatiosteres* End.; *Philoliche* Wied. (syns. *Nuceria* Walk., *Metaphara* End.); *Stenophara* End.; *Dorcaloemus* Aust.; *Phara* Walk.; *Subpangonia* Surc.

Oriental and Northern Australasian — *Philoliche* Wied.

I. INTRODUCTION

In Part I of this series (Mackerras 1954), a new classification of the Tabanidae was proposed, and the evolution and distribution of the family were reviewed. It remains now to examine the basis of the classification more closely, to discuss the scope and content of the tribes, and to give notes on the genera studied. As I can accept responsibility for identification of Australasian species only, the names of the identifying authorities, where known, are included after the names of species listed from other parts of the world in the systematic sections of the paper.

In order to keep each Part of this series to a reasonable size, the present paper will be limited to a discussion of general systematic problems and the subfamily Pangoniinae. The subfamilies Scepsidinae, Chrysopinae, and Tabaninae will be reserved for later Parts, which will conclude with a short account of the faunal composition of the several regions to complement the more general zoogeographical discussion in the first paper.

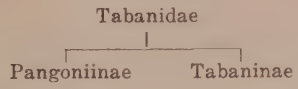
It will be necessary to describe three new Australian species in the present paper, as they are the types of two genera and a subgenus which should be recorded in a work of this kind.

* While this paper was in press, information was received from Mr. Oldroyd that he had gone carefully into the history of all the supposedly African specimens of *Scaptia*. He had found that there was no good evidence that any of them actually came from Africa—they may well have been mis-labelled. No recent specimens have been taken, and *Scaptia* must therefore be deleted from the Ethiopian list until evidence to restore it is produced. All references to the occurrence of *Scaptia* in Africa should, therefore, be ignored in this paper, and the map already published (Mackerras 1954, Fig. 6) corrected accordingly.—I.M.M., 10.viii.1955.

II. Historical Background

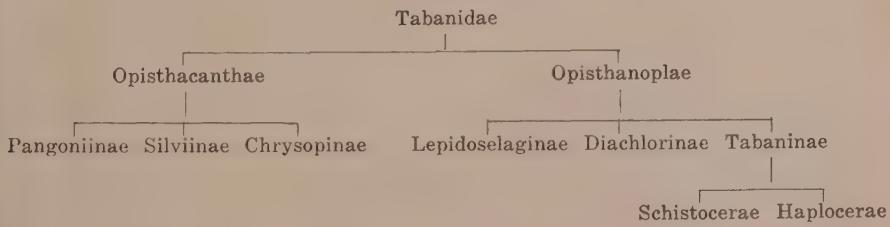
Loew (1860) was the first to divide the family Tabanidae into two subfamilies, Pangoniinae and Tabaninae, on the presence or absence respectively of paired spurs on the hind tibiae. Workers over the ensuing 60 years added genera and species, but almost all accepted his primary divisions without question. This period of simplicity culminated in Surcouf's (1921) treatment of the family in the *Genera Insectorum*.

Loew (1860) to Surcouf (1921)



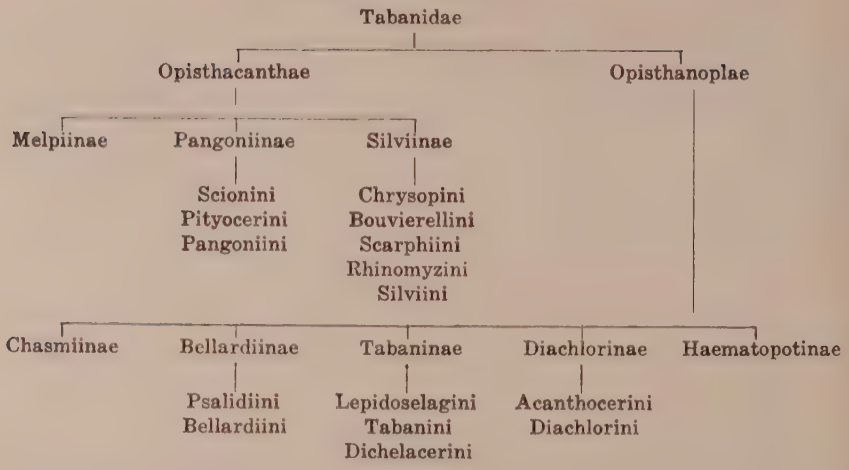
Lutz alone seemed to feel the need to recognize a greater number of natural groups. In 1905, in a paper of which Dr. Fairchild has kindly sent me extracts, he pointed out that the genera centring on *Chrysops*, although agreeing in possessing hind tibial spurs, differed considerably in other respects from those centring on *Pangonia*, and he separated them as the subfamily Chrysopinae. He still wished to retain the old primary dichotomy, however, so in 1909 he raised Loew's subfamilies to sectional rank as Opisthacanthae, with three subfamilies, and Opisthanoplae, which he subdivided similarly in 1913. His complete arrangement is shown below.

Lutz (1909, 1913)



Lutz's work was a serious attempt to separate out natural groups of manageable size, but it was almost completely ignored, until Enderlein (1922, 1925) based his elaborate classification on it. The 1922 arrangement was slightly the simpler, and is shown here, the Pelecorhynchinae, which are discussed later, being omitted from this and subsequent diagrams. He apparently did not know of Lutz's (1905) paper, which invalidates his selection, as first reviser, of Silviinae in preference to Chrysopinae. Otherwise his nomenclature was correct at the time, although his choice of little known genera as types of some of his tribes was unfortunate.

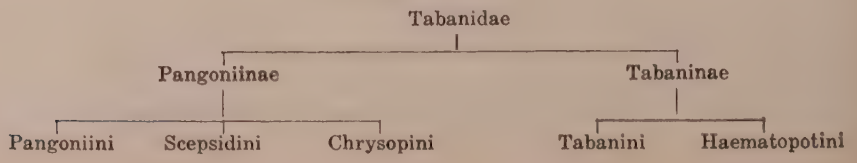
Enderlein (1922)



It is not too harsh to say that Enderlein's classification was entirely artificial. He used single characters almost throughout, made no attempt to correlate them with other characters, ignored parallel evolution, and took little account of variability. His arrangement was criticized by Bequaert (1924), Szilàdy (1926) and Ferguson (1926), and ignored by Schuurmans Stekhoven (1926) ; but it was accepted by several continental workers, of whom Séguy (1926) and Kröber (1932, 1939) were the chief. Kröber (1930*b*, 1932) amalgamated Melpiinae with Pangoniini, and he also (Kröber 1930*a*) created a new subfamily, Stenotabaninae, for generalized Opisthanoplae which lacked a tooth or sharp angle on the third antennal segment. However, he was still wedded to the single character principle, and even went so far (Kröber 1930*b*) as to exclude *Demoplatus* (= *Caenoprosopon*) from the Opisthacanthae, because it sometimes lacks hind tibial spurs.

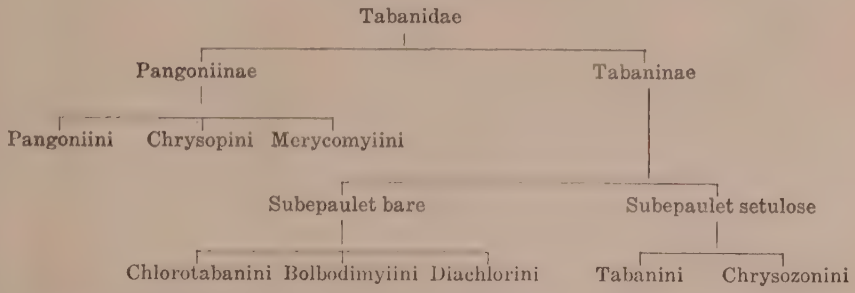
This period of artificiality was followed by one in which relationships were assessed on a broader basis. Bequaert (1930) began it by reverting to Loew's subfamilies and proposing a simple arrangement of tribes, in which the Scepsidini were recognized for the first time as a separate group. However, only *Chrysops* was included in the Chrysopini, and the remainder of Enderlein's Silviinae were left in the Pangoniini.

Bequaert (1930)



Philip (1941*a*) was responsible for further advances. Working on the Nearctic fauna, he was led naturally to include *Silvius* and *Assipala* with *Chrysops* in the Chrysopini, and he recognized another distinctive element, the Merycomyiini, which we now know to be more widely distributed. More important, he employed the presence or absence of setulae on the basicosta (subepaulet) to mark a major line of cleavage in the Tabaninae. His plan, as applied to the Nearctic fauna and amended in 1947, is shown in the following diagram.

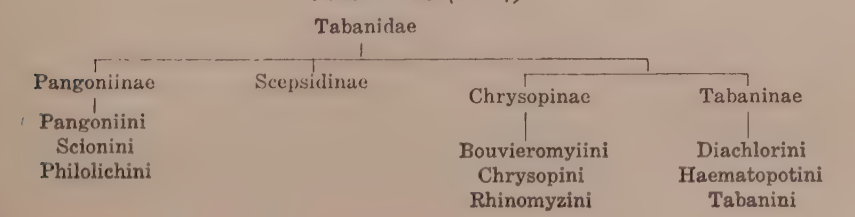
Philip (1947)



Fairchild (1942*b*) did not accept the Chlorotabanini as distinct from the Dichelacerini, but recognized the Lepiselagini as an additional Neotropical element. Several other tribes would also need to be added if Philip's plan were to be carried to its logical conclusion in other parts of the world.

It is apparent from this review, firstly, that Loew's initial dichotomy has remained unchanged throughout all the systematic vicissitudes of the family; secondly, that the concept of subfamilies and tribes has found favour with modern workers; and thirdly, as Oldroyd (1949) has pointed out, that some of Enderlein's groups do have a natural basis, although they need redefinition. The two principal characters employed have been the presence or absence of hind tibial spurs and the consolidation of the third antennal segment. Both have been found to have limitations and sometimes to obscure relationships. Hypopygial characters were therefore used as a guide to what is believed to be a more natural arrangement, which is set out below for comparison with the earlier diagrams.

Mackerras (1954)



III. Morphology

It is not proposed to review all the characters that have been used at suprageneric levels in the Tabanidae, but the genitalia of both sexes have proved to be so important that it seems desirable to describe them in some detail. Most of the external characters will come up for discussion in later sections, and it is only necessary to state here that a conservative terminology is used almost throughout, purely because it should readily be understood by most workers, and without prejudice to questions of homology. A more modern view, with excellent illustrations and a full bibliography, has been given by Pereira Barretto (1946).

Male Genitalia

The information provided by the male genitalia has already been stated in Part I of this series. They indicate clearly, I believe, the major lines of evolution in the family, but, with comparatively few exceptions, they are of little value for the finer distinctions between genera and species. This is an unusual state of affairs, which probably explains why those who have examined them previously (e.g. Cole 1927; Bouvier 1940) have thought them to be of little value.

I have not had much success in drawing out the parts after relaxation, and find it best to sacrifice the terminal 3rd or 4th of the abdomen by snipping it off with a pair of fine scissors. The detached portion is then boiled in 10 per cent. KOH for about 15 minutes, passed through water, two changes of glacial acetic acid, two changes of clove oil (10-15 minutes at each step), and mounted in balsam.

Dissection is done under Greenough binocular microscope in the second change of oil. The basal segments are removed, and usually discarded. The 9th tergite and parts attached to it are dissected off, and the residual tissues and tracheae cleaned out from both dorsal and ventral parts, before mounting them between coverslips cemented to a piece of card. This is attached to the pin carrying the specimen, so that the parts are always associated with the insect from which they came. A further advantage of this method is that the dorsal and ventral surfaces can be examined equally readily under high power. In the present paper, all the drawings, unless otherwise stated, are of the dorsal view.

Taking *Scaptia* (Fig. 1*A-C*) as an example, the 9th tergite forms a shield overlying the aedeagus and clasping organs. There is no evidence of rotation. The 10th tergite has disappeared, but its position can be indicated by examining the corresponding structures in *Pelecorhynchus* (Mackerras and Fuller 1942). The cerci (*c*) and 10th sternite or proctiger are broadly similar to those of other members of the superfamily.

The 9th sternite is fused with the bases of the gonocoxites (*gc*), which are well developed, but simple in form, and without accessory structures other than the terminal style (*s*). The aedeagus (*aed*) lies between the bases of the coxites; it is a relatively simple conical tube, with reinforced lateral walls, and containing the penis and flagella (*fl*) with their

associated muscle struts. The flagella are present in all members of the family, and are almost characteristic of it, although they are also developed in a few Rhagionidae.

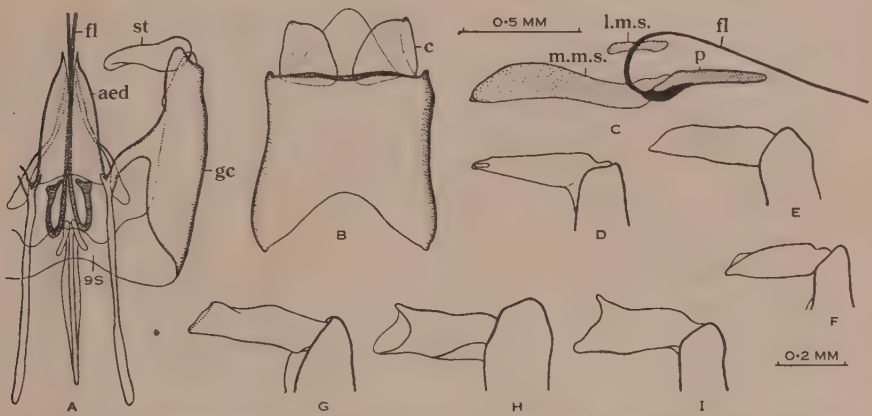


Fig. 1.—*A-C, Scaptia patula* (Walk.), Australia: *A*, ♂ genitalia. *9S*, 9th sternite; *aed*, aedeagus; *fl*, flagellum; *gc*, gonocoxite; *st*, style. *B*, Ninth tergite and associated parts. *c*, cerci. *C*, Lateral view of penis (*p*), flagellum (*fl*), and muscle struts (*l.m.s*, *m.m.s*). *D-I*, Styles of: Chrysopinae — *D*, *Pseudotabanus fergusoni* (Ric.), Australia; *E*, *Veprius presbiter* Rond., Chile; *F*, *Tabanocella denticornis* (Wied.), Africa. Tabaninae — *G*, *Protodasyommia sarpa* (Walk.), New Zealand; *H*, *Tabanus bovinus* Linn., Europe; *I*, *Stibasoma theotenia* (Wied.), South America. (For styles of Pangoniinae, see Mackerras 1954, Fig. 3.)

The character of most value is found in the 9th tergite, which forms a single shield in the Pangoniinae, and is clearly divided into two parts in the other subfamilies. This character has been almost completely uniform in the material examined, the only exceptions being African species of *Mesomyia* and *Aegophagamyia,* in which the tergite is incompletely divided though of normal chrysopine shape. There are small differences in the coxites and aedeagus, and the flagella vary in size in some of the groups. The shape of the style is more useful, being single or bifid in Pangoniinae (Mackerras 1954, Fig. 3), more or less pointed in dorsal view in Chrysopinae (Fig. 1*D-F*), and always characteristically truncate in Tabaninae (Fig. 1*G-I*). Care is necessary in examining these parts, as their shape may vary appreciably according to the angle at which they are viewed.

Female Genitalia

The terminal segments of the female have supported the conclusions drawn from the male. The method of dissecting and mounting is similar, except that the 8th sternite is dissected away from all the parts that overlie it, the genital fork and spermathecal ducts being left attached either dorsally or ventrally. I find it difficult to decide which is the more convenient, but the former is usually a less tricky dissection.

These segments are nearly always dorsoventrally compressed, occasionally laterally compressed, but never of the tubular form characteristic of *Pelecorhynchus* and most Rhagionidae. There is no evidence of rotation.

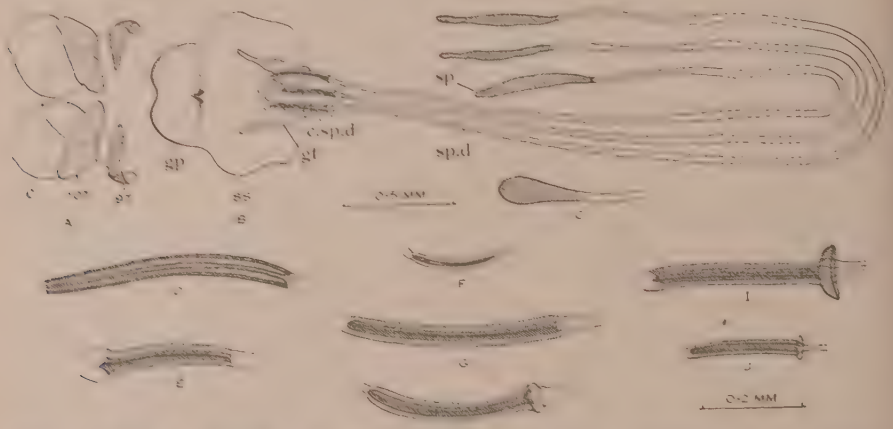


Fig. 2.—*A-B*. ♀ genitalia of *Cydistomyia doddi* (Tayl.), Australia: *A*, terminal segments. *9T*, ninth tergite; *10T*, tenth tergite; *c*, cerci. *B*, Eighth sternite and associated parts, viewed from above. *8S*, eighth sternite; *gp*, anterior gonopophyses; *gf*, genital fork; *c.sp.d*, caudal ends of spermathecal ducts (*sp.d*); *sp*, spermathecae. *C*, Spermatheca of *Tabanus bovinus*. *D-J*, Caudal ends of spermathecal ducts of: Pangoniinae — *D*, *Scaptia maculiventris* (Westw.), Australia; *E*, *Stonemyia tranquilla* (O.-S.), North America. Scepsidinae — *F*, *Scepsis nivalis* Walk., South America. Chrysopinae — *G*, *Mesocomyia whitneyi* (Johns.), North America; *H*, *Veprius presbiter*. Tabaninae — *I*, *Tabanus bovinus*; *J*, *Heptatoma pellucens* Fabr., Europe.

The 9th tergite (Fig. 2*A*) shows the same differences as in the male, but even more marked, being a continuous transverse bar in the Pangoniinae, but a pair of widely separated, triangular, lateral plates in Chrysopinae and Tabaninae. This character also is not quite constant, in that the tergite tends to split in some African Pangoniinae, and is distinctly divided in 2 of the 3 species of *Phara* that I have examined. The 10th tergite (*10T*) is nearly always divided, and varies considerably, even within species, in the extent to which it is chitinized. The 10th sternite is normal, and the cerci (*c*) 1-segmented, which differentiates the Tabanidae from primitive Tabanoidea.

On the ventral surface, the 8th sternite (*8S*) and anterior gonopophyses (*gp*) form a strong shield, which shows some interesting variations. The genital fork or furca (*gf*), lying dorsal to the 8th sternite, is usually large and irregular in shape, and the spermathecal ducts meet in an ampulla on its dorsal surface (see *Mycteromyia*, Fig. 23).

There are 3 spermathecae, which are more or less deeply pigmented, oval or fusiform in shape in all subfamilies, and lie about the level of the 6th or 7th abdominal segment, though sometimes more posteriorly. They are often lost in dissection. The ducts are very long, slender, and

lightly chitinized; they extend anteriorly for a considerable distance, and then bend back on themselves to run nearly to the tip of the abdomen. At their posterior ends, just before they enter the common ampulla, their walls are generally strengthened in a characteristic way. In the Pangoniinae (Fig. 2*D*, *E*), Scepsidinae (Fig. 2*F*), and Chrysopinae (Fig. 2*G*, *H*) the strengthening usually consists of chitinous thickenings, so that the ducts rather resemble tracheae, and there are at most slight funnel-shaped expansions. In some Pangoniini, they are so delicate, that they can only be seen clearly by phase-contrast microscopy. In *Mycteromyia* (Fig. 23), each duct has a curious little blind diverticulum. In the Tabaninae, this portion of the duct is quite strongly chitinized, and ends in a characteristic mushroom-shaped expansion (Fig. 2*I*, *J*), which is always present, and which I have not seen in any other group.

Thus, Pangoniinae can be separated by the 9th tergite, and Chrysopinae from Tabaninae by the caudal ends of the spermathecal ducts. The Scepsidinae seem to be quite peculiar, and will be discussed in Part III (Mackerras 1955).

An important paper by Ovazza and Taufflieb (1954) reached Australia after the above was written. They did not recognize the 9th tergite, but they saw the delicate little cups on the caudal ends of the spermathecal ducts (*"manchons"*) of Tabaninae, and concluded that they are characteristic of that subfamily. They supported the removal of *Thaumastocera* from the Tabaninae, because it was found to have simple *"manchons"*. They also attached more importance to the shape of the furca and the arrangement of the small groups of hairs at the caudal ends of its limbs than I have so far been able to give these structures in the present study.

IV. The Early Stages of Tabanidae

The early stages of so few Tabanidae are known, that it will be convenient to summarize the available information here, leaving later sections almost entirely to consideration of adult characters. So far as I can find, representatives of only 12 genera have been described in sufficient detail for comparative purposes. These are shown in the following tabular statement, and some Australian examples are illustrated in Figure 3.

Pangoniinae		
Pangoniini	:	*Ectenopsis*
Scionini	:	*Scaptia, Goniops*
Philolichini	:	—
Scepsidinae	:	—
Chrysopinae		
Bouvieromyiini	:	*Lilaea*
Chrysopini	:	*Chrysops*
Rhinomyzini	:	—
Tabaninae		
Diachlorini	:	*Dasybasis, Lepiselaga*
Haematopotini	:	*Haematopota*
Tabanini	:	*Tabanus, Hybomitra, Atylotus, Euancala*

It is clear that our knowledge is too meagre to warrant any firm conclusions, but Miss K. M. I. English, of the Department of Zoology,

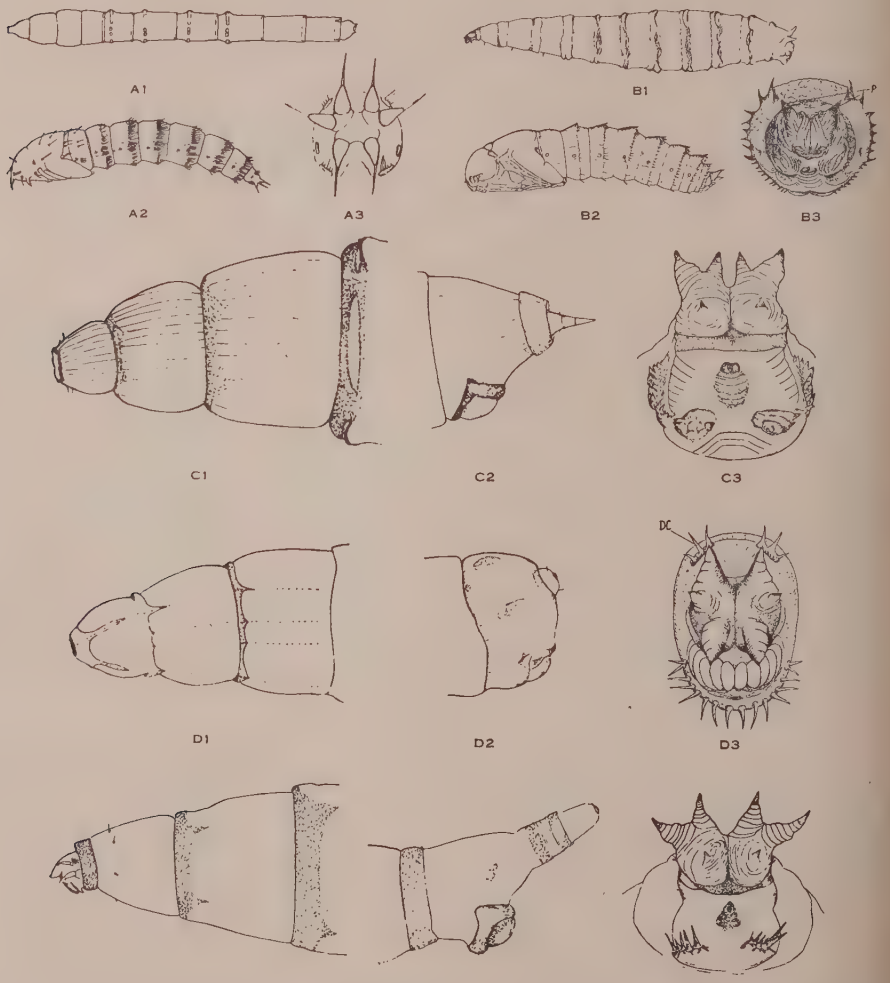


Fig. 3.—Early stages of Australian Tabanidae. *A*: 1, lateral view of larva; 2, lateral view of pupa; 3, aster, of *Ectenopsis angusta* (Macq.) (from English 1953). *B*: Same of *Scaptia auriflua* (Walk.) (from Fuller 1936). *C*: 1, head of larva, 2, tail of larva, 3, aster, of *Lilaea notata* (Ric.) (from Hill 1921). *D*: Same of *Dasybasis froggatti* (Ric.) (from Fuller 1937). *E*: Same of *Tabanus pallipennis* Macq. (= *rufinotatus* Big.) (from Hill 1921).

University of Sydney, who is working intensively on the Australian species, has drawn my attention to some interesting facts. I am very much indebted to Miss English for her contribution to this discussion.

(1) The known pangoniine larvae are distinguished from all others, not only in body form, but in having fleshy processes on the 8th abdominal segment, the distal end of the maxilla long and slender, the prothoracic annulus covered with setulose scales (fine setulae only in Chrysopinae and Tabaninae), and possibly in having the fleshy part of the labium large and hairy. The pupae of *Scaptia* and *Goniops* are also sharply distinguished by having an aster with only 2 projections. That of *Ectenopsis angusta* (Macq.), on the other hand, has the normal 6 projections (English 1953), but both groups differ from Chrysopinae and Tabaninae in thoracic chaetotaxy.

(2) Chrysopine larvae do not resemble those of Pangoniinae, but are much closer to Tabaninae, from which they can usually be distinguished by having the chitinous part of the posterior spiracle produced into a spike posteriorly. Hennig (1952) agrees with this view, saying (in translation): "It is, therefore, of great interest that in the larval morphology an important cleavage lies not between the Opisthacanthae and Opisthanoplae, as these groups are distinguished according to the adults, but between the Pangoniinae and the Silviinae (*Chrysops*)"; and later, under Silviinae: "It is very remarkable that the larvae are very much more like those of the Tabaninae than the larvae of the Pangoniinae". The pupae are also similar in both groups, having well-developed asters and other characters in common, but differing from one another in thoracic and abdominal chaetotaxy.

(3) The larvae of the Australian *Dasybasis* differ from *Tabanus* larvae and agree with those of *Haematopota* in lacking a siphon on the 8th abdominal segment.

V. Limits of the Family

For a long time, the Chilean-Australian genus *Pelecorhynchus* was placed in the Tabanidae, and occasionally other primitive genera were associated with it. Bequaert (1930) and Philip (1941*a*) recognized its isolated position, and a separate family, Pelecorhynchidae, was erected for it by Mackerras and Fuller (1942). This action was accepted by Philip (1947), but not by Hardy (1944), while Steyskal (1953) included it in the Coenomyiidae. Dr. Philip has kindly lent me a female of the related Nearctic *Bequaertomyia anthracina* Bren. It has similar genitalia, and differs from *Pelecorhynchus* chiefly in having hairy eyes and a more elongate cell R_4 (Fig. 4*H*), which is an additional indication that the relationships of the group do not lie with the Tabanidae.

Another genus to be excluded is the Chilean *Heterostomus*, which was considered to be a pangoniine by Kröber (1930*b*, 1932), although Malloch (1932), in the same series as Kröber's first paper, included it in the Rhagionidae. Again through the kindness of Dr. Philip, I have been able

to examine a pair of the genotype, *H. curvipalpis* Big. (det. Philip), and can confirm that it is not a tabanid, on the following grounds:

Ocelli arranged in an elongate triangle (Fig. 4B), which is not seen in the Tabanidae.

Proboscis very short and fleshy, with large labella (Fig. 4A), more like *Pelecorhynchus* and some Rhagionidae than Tabanidae.

Legs with single apical spurs on fore tibiae, as well as paired spurs on mid and hind.

Wing with cell R_4 long and narrow, and vein R_1 ending at wing tip (Fig. 4D). Cell Cu_2 is closed, but vein A_1 is arched, and the general appearance of the venation is unlike that of Tabanidae.

Squamae rudimentary.

Male hypopygium (Fig. 4E, F) unlike any tabanid in shape of coxites, style, and aedeagus, and without flagella.

Female hypopygium (Fig. 4G) sharply distinguished by having 2-segmented cerci. The 8th sternite is peculiar in being largely membranous, with the chitinized parts forming a pair of separated plates.

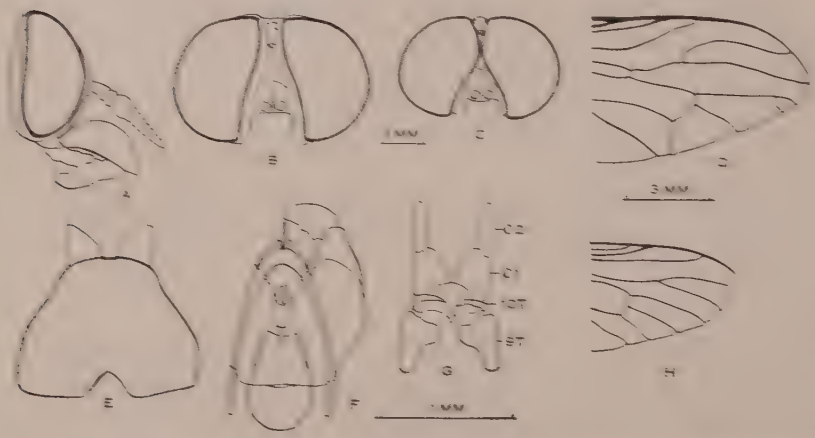


Fig. 4.—*Heterostomus curvipalpis* Big., Chile: *A*, *B*, head of ♀; *C*, head of ♂; *D*, apex of wing of ♀; *E*, ninth tergite of ♂; *F*, ♂ genitalia; *G*, terminal segments of ♀ (lettering as in Fig. 24, except *st*, *st*2, first and second segments of cerci). *H*, Apex of wing of *Bequaertomyia anthracina* Bren., ♀, North America.

This is not the place to discuss the correct position of *Heterostomus*; Steyskal (1953) places it in Erinnidae.

Another genus which merits brief attention is the Australian *Spaniopsis*. The species are blood-suckers, have well-developed mandibles in the female, apical spurs on mid tibiae only, and, except for their large ocelli, they look like small tabanines. However, the squamae are rudimentary, cell R_4 is long and narrow, the 3rd antennal segment is entirely

without annulations, the cerci of the female are 2-segmented, the aedeagus of the male lacks flagella, and the general form of the genitalia (Fig. 5*D, E*) resembles Rhagionidae rather than Tabanidae. There is no doubt that the genus was correctly placed by Ferguson (1915).

Dr. Philip has also sent me a female of the blood-sucking Nearctic rhagionid, *Symphoromyia atripes* Big. As can be seen from the profile of the head (Fig. 5*G*), it is not closely related to *Spaniopsis*, so it is evident that the blood-sucking habit developed independently at least twice in the Rhagionidae as well as in the Tabanidae.

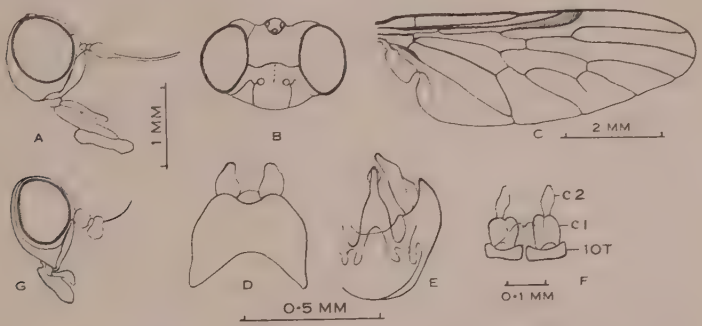


Fig. 5.—*Spaniopsis longicornis* Ferg., Australia: *A, B*, head of ♀; *C*, wing of ♀; *D, E*, ♂ genitalia. *F, Spaniopsis vexans* Ferg., Australia, terminal segments of ♀ (lettering as in Fig. 4*G*). *G, Symphoromyia atripes* Big., North America, head of ♀.

As limited by the exclusion of these genera, the family Tabanidae remains compact and structurally homogeneous. It may be defined as follows:

Adult

Empodia pulvilliform; thorax and abdomen often with long silky hairs, but never with strong macrochaetae.

Antennae porrect; 3rd segment annulate, usually with 5-8 annuli, very rarely reduced to 2 or 1; style, when differentiated, relatively short and stout, never thin and bristle-like.

Proboscis (except in Scepsidinae) strong, and labium more or less chitinized and rigid; mandibles (except in some Rhinomyzini*) well developed in ♀, absent in ♂.

Apical spurs absent on fore tibiae, present on mid, present or absent on hind. Wing with costa continuous round posterior margin; 4 radial and medial veins (Tillyard notation); *Rs* originating proximal to base of discal cell; cell R_4 short and wide, vein R_5 ending behind apex; vein *An* straight, cell Cu_2 usually closed. Squamae well developed.

* Mr. Oldroyd has informed me that females of *Thaumastocera* and *Sphecodemyia* have no mandibles. It would be desirable to dissect other species that do not suck blood.

♂ hypopygium with 9th tergite single or divided; 10th tergite absent; aedeagus a conical tube; flagella developed; style simple or bifid. ♀ hypopygium with 9th tergite single or divided; 10th tergite usually divided; cerci 1-segmented; 8th sternite a chitinized shield.

For general purposes, the habitus, venation, strong proboscis, characteristic antennae and presence of squames will almost always serve to distinguish Tabanidae from related families. The cerci are 2-segmented in the females of *Pelecorhynchus, Bequaertomyia,* Rhagionidae *Heterostomus, Coenomyia,* and primitive Stratiomyiidae, an important point of differentiation.

Pupa

Free. Head with antennal sheaths directed laterally. Prothorax with a pore opening into a large aperture medial to and connected with the spiracle, which is usually curved and ear-shaped. Abdominal armature consisting of 1, or 2 closely contiguous, series of bristles on each segment except the 1st dorsally, and a weaker transverse series ventrally. Aster on last segment well developed, with 2 or 6 projections.

Larva

Head retractile; body spindle-shaped, truncate, or club-shaped, circular or somewhat compressed in cross section; surface usually longitudinally striate; abdominal segments with more or less well-developed pseudopodia. Mandibles strong, hook-like, down-curved; maxillae well developed, wholly or largely membranous; palpi well developed; antennae distinct, pedunculate, 2- or 3-segmented. Graber's organ developed, sometimes hidden. Anterior spiracles non-functional; posterior spiracles closely approximated, lying in a vertical stigmatal slit or area; siphon present or absent.

VI. Primary Classification

The evolution and relationships of the principal subdivisions in the family have already been discussed in Part I. It remains here to present a key to the subfamilies, based as far as possible on external characters, and to note two points of practical difficulty, which will be encountered by the worker who is reluctant to dissect his material.

Key to Subfamilies of Tabanidae

1. Proboscis and mouth-parts minute; palpi small, globular in both sexes; 3rd antennal segment with 6-8 annuli ..... Scepsidinae

   Proboscis and mouth-parts well developed; palpi never small and globular in both sexes 2

2. Third antennal segment with 6-8 distinct annuli; hind tibial spurs nearly always present; 9th tergite entire in both sexes ..... Pangoniinae (pt.)

   Third antennal segment with never more than 5 distinct annuli 3

3. Ocelli usually absent, small or rudimentary if present; hind tibial spurs absent; 9th tergite divided in both sexes; style of ♂ hypopygium truncate; caudal ends of spermathecal ducts of ♀ with mushroom-like expansions ..... Tabaninae

Ocelli well developed; hind tibial spurs usually well developed, sometimes small, rarely absent; style of ♂ hypopygium never truncate; caudal ends of spermathecal ducts of ♀ never with mushroom-like expansions 4

4. Ninth tergite entire in both sexes; style of ♂ hypopygium bifid .. Pangoniinae (pt.)
Ninth tergite divided in both sexes;* style of ♂ hypopygium single, more or less pointed in dorsal view ..... Chrysopinae

The first of the potential difficulties concerns the hind tibial spurs, which still remain a valuable subsidiary character. It is worth emphasizing their incomplete constancy, because they have been given such weight in the past. In the Pangoniinae, they vary down to vanishing point in the Australian genus *Caenoprosopon*. In the Chrysopinae, they are very small in the Nearctic *Merycomyia*, which was originally thought to be a tabanine, and they are sometimes so small as to be difficult to detect in Australian species of *Pseudotabanus*; they are absent in the African *Thaumastocera*, which (Mr. Oldroyd informs me) proved to be a chrysopine when dissected. No tabanine with spurs is known, although the Neotropical *Triceratomyia* was thought to possess small spurs when it was described.

The uncertainty in distinguishing between Chrysopinae and Tabaninae is sometimes real, owing to the close superficial resemblance between many members of the two subfamilies, which makes reliance on the strictly diagnostic characters essential. In this connection, it is useful to remember that, with the removal of *Metaphara*, there is no chrysopine known without well-developed ocelli.†

The second difficulty concerns that group of the Pangoniini, in which the basal part of the 3rd antennal segment has become more or less completely compacted and the apical annuli reduced to 4 or fewer. This group is absolutely characterized by the hypopygial characters given in the key, but superficially it is almost indistinguishable from some generalized Bouvieromyiini. It includes the Nearctic *Asaphomyia* (possibly *Zophina*), the Neotropical *Chaetopalpus* (possibly *Histriosilvius*) and the Australasian *Parasilvius*, *Paranopsis*, and *Therevopangonia*. The superficial aids to its recognition are weak, being limited to the presence of a well-developed appendix on R_4, absence of a callus, and some rather subtle suggestions in general appearance, shape, and hairiness of palpi, etc. Any insect with these characteristics is well worth dissecting.

VII. Nomenclature

Many names have been used for the subfamilies and tribes of Tabanidae. In selecting those to be retained, I have endeavoured to follow the "Copenhagen Decisions on Zoological Nomenclature," published by

* Rarely narrowly united in mid-line in ♂.

† Schuurmans Stekhoven (1926, 1932) described four species of "*Silvius*" from New Guinea and one from Celebes as without well-developed ocelli and with the hind tibial spurs "inconspicuous". I feel sure that he was mistaken and was really dealing with species of *Cydistomyia*.

the International Trust for Zoological Nomenclature, 1953, pp. 32-7. It follows that the oldest valid family-group name which is based on an included genus must be used, irrespective of whether or not the revised category differs in content from its predecessor, or whether the type genus is at all central in its new association. This will inevitably cause temporary confusion and inconvenience; but I do not think it serious enough to justify application for conservation of more appropriate names, and in any case it might be difficult to induce all one's colleagues to accept a set of names chosen less objectively.

For convenience, the complete list will be presented here, and synonymy will not be repeated in later sections. Where applicable, the original author of a name and the year from which it dates are given in brackets, followed by the name and date of the author who first used it at its altered taxonomic level.

Explanation of one name is necessary. Of the three names (all proposed by Enderlein 1922), which are available for the second tribe of Pangoniinae, the first, Melpiinae, is based on a subjective synonym. It is likely to remain so, and it would be inconvenient to workers on the family to resurrect it to replace the well-known *Fidena* Walk. I have therefore (Mackerras 1954) selected the second name, Scionini, based on a clearly defined type genus, as the name of the tribe.

Synonymy of Tribes of Tabanidae

Pangoniinae Loew, 1860.
Pangoniini (Loew, 1860) Enderlein, 1922.
Scionini Enderlein, 1922.
Melpiinae Enderlein, 1922.
Pityocerini Enderlein, 1922.
Philolichini Mackerras, 1954.

Scepsidinae (Bequaert, 1930) Mackerras, 1954.
Scepsidini Bequaert, 1930.

Chrysopinae Lutz, 1905.
Silviinae Lutz, 1909.
Chrysopini (Lutz, 1905) Enderlein, 1922.
Silviini (Lutz, 1909) Enderlein, 1922.
Bouvieromyiini (Enderlein, 1922) emend. Séguy, 1949.
Bouvierellini Enderlein, 1922 (based on nom. preocc.).
Scarphiini Enderlein, 1922.
Scarphiinae Enderlein, 1925.
Merycomyiini Philip, 1941.
Rhinomyzini Enderlein, 1922.

Tabaninae Loew, 1860.
Tabanini (Loew, 1860) Enderlein, 1922.
Bellardiinae Enderlein, 1922.
Bellardiini Enderlein, 1922.
Haematopotini (Enderlein, 1922) Bequaert, 1930.
Haematopotinae Enderlein, 1922.
Chrysozoninae Kröber, 1939.
Chrysozonini (Kröber, 1939) Philip, 1941.

Diachlorini (Lutz, 1913) Enderlein, 1922.
Diachlorinae Lutz, 1913.
Lepidoselaginae Lutz, 1913.
Lepidoselagini (Lutz, 1913) Enderlein, 1922.
Lepiselagini (Lutz, 1913) emend. Fairchild, 1942.
Chasmiinae Enderlein, 1922.
Psalidiini Enderlein, 1922.
Dichelacerini Enderlein, 1922.
Acanthocerini Enderlein, 1922.
Stenotabaninae Kröber, 1930.
Stenotabanini (Kröber, 1930) Philip, 1941.
Bolbodimyiini Philip, 1941.
Chlorotabanini Philip, 1941.

Notes: (i) Lutz used Selasominae loosely in 1913 and 1928 as interchangeable with Lepidoselaginae; it cannot be regarded as having been validly proposed.

(ii) Lutz's (1913) names may possibly date from 1909 or 1911, when they were used in papers of doubtful status under the Rules (see Fairchild 1950; Pereira Barretto 1950).

VIII. Assessment of Genera

The systematic worker, who attempts to assess generic levels in the Tabanidae, is faced with the practical difficulty that there are several different sorts of genera in the family.

(i) A comparatively small number of clearly defined, usually small, probably ancient genera, such as *Goniops, Chaetopalpus, Phara,* and *Austroplex.*

(ii) A comparatively small number of usually small, usually tropical genera, which are characterized by some striking aberration, for example, *Pityocera, Gastroxides, Bolbodimyia, Paracanthocera.* .

(iii) Ancient genera, which are in process of breaking up, for example, *Ectenopsis, Scaptia, Mesomyia, Dasybasis.* This group is parallel to the next.

(iv) More recent genera, which are clearly distinct at their extremes, but merge together in the middle, *Chrysops* and *Silvius* being a striking example.

(v) Offshoots from the larger recent groups, recognizable by well-defined (e.g. *Whitneyomyia, Efflatounanus*) or minor but fairly constant characters (e.g. *Atylotus*).

The situation is further complicated by the large number of species in the family, repeated parallel evolution, paucity of structural characters, and the fact that segregates are sometimes quite distinct in one region but merge together in another, so that workers in different regions would naturally have different opinions about their validity.

These difficulties have led to differences of emphasis, some feeling that all recognizable natural groups should be named, even if it is difficult to place the intermediate species, others believing that there is so much

fusion of genera that many at present accepted are useless. Even genera which do not show fusion are often regarded with suspicion, because many of them are monotypic or contain but few species. The Australian *Ectenopsis* and *Parasilvius* (q.v.) are a good example of what may happen, and a similar position may be arising in the unspecialized Nearctic Pangoniini.

This is a situation which, I believe, no amount of searching for new characters will overcome. It is a natural evolutionary phenomenon, and the old conflict between the "lumpers" and "splitters" has here the added point that it is based, not merely on interpretation, but on reality. There would seem to be only one answer to this problem, within the framework of existing taxonomic practice: to recognize a comparatively small number of better characterized genera, and to reduce to subgeneric level those less definable natural groups which it is still desirable to identify by a name.

There is nothing new in this. Quite a number of workers, Fairchild in particular, have proposed subgenera in the Tabanidae very much in the way that is suggested here. All that is attempted now is to extend the principle more widely. As, however, I am averse to interfering with the status of genera from other regions, which I only know superficially, most changes will be suggested, rather than formally made, leaving the final decision to workers with local knowledge. Definite synonymy will only be proposed when genotypes have been compared.

IX. Subfamily **PANGONIINAE** Loew, 1860

Ninth tergite an undivided chitinous shield in ♂; almost always a single transverse bar in ♀. Ocelli well developed (except in African genera). Antennae short, little if at all longer than the antero-posterior diameter of the head; 1st and 2nd segments short; 3rd usually subulate, sometimes with basal annuli swollen, usually 6-8-annulate. Hind tibiae with paired apical spurs (sometimes minute, occasionally not detectable). Vein *sc* bare above and below. Style of ♂ hypopygium single or bifid, finger-like or pointed. Caudal ends of spermathecal ducts of ♀ without mushroom-like expansions.

The general appearance is very variable. Many are stout, bombyliid-like flies, with long, sometimes exceedingly long, proboscis; others are more parallel-sided; and some are quite elongate and narrow-bodied. The frons usually diverges towards the antennae, and is smooth or wrinkled; a callus is uncommon, and, when present, it is rarely prominent. The legs are nearly always relatively long and slender, as compared with other subfamilies, and they seem well adapted to clinging to flowers.

During the survey of the male and female genitalia, it was found that the Pangoniinae could be divided into three sections on hypopygial characters. These characters were sex-linked, and consequently had the disadvantage that one section could be identified with precision only from

males, and another only from females; but they were quite constant in the material examined, there was good, though not complete, correlation with external characters, and they clearly represented ancient, well-stabilized cleavages within the subfamily. They were actually better defined than groups which had been given tribal rank in other subfamilies, and it was therefore decided to recognize them as tribes. They can be distinguished as shown in Part I (Mackerras 1954, Fig. 3), and by the following key.

KEY TO THE TRIBES OF PANGONIINAE

1. Style of ♂ hypopygium bifid. Gonopophyses of ♀ not widely separated. Ocelli present; eyes usually bare; R_4 nearly always with strong appendix. Palaearctic, Nearctic, Neotropical, Australasian ..... Pangoniini

   Style of ♂ hypopygium simple 2

2. Gonopophyses of ♀ not widely separated. Ocelli present; eyes nearly always hairy; appendix on R_4 variable, usually absent. Nearctic, Neotropical, southern Ethiopian, Australasian ..... Scionini

   Gonopophyses of ♀ widely separated, and distal edge of 8th sternite strongly chitinized. Ocelli absent (except *Buplex*); eyes bare; R_4 nearly always with strong appendix. Ethiopian, Oriental, northern Australasian ..... Philolichini

The exceptions are worth noting. In the Pangoniini, *Stonemyia* lacks an appendix to R_4, while *Brennania, Pilimas, Asaphomyia, Chaetopalpus,* and *Parasilvius* have more or less hairy eyes; the last 3 have the basal annulations of the 3rd antennal segment fused, a condition which has not been seen in the other tribes. In the Scionini, *Goniops* and *Mycteromyia* have bare eyes, and the latter has quite a strong appendix to R_4. The female of the Australian *Scaptia conspicua* (Ric.) also has bare eyes, although the male is normal, and some species of *Scaptia* have a small, usually inconstant appendix to R_4. In the Philolichini, *Buplex* has well-developed ocelli, and *Subpangonia* only a rudimentary appendix to R_4, but both are typical members of the tribe in other respects.

These inconsistencies in external characters make dissection essential for precise determination. Some genera cannot be placed, even tentatively, from their descriptions, and these are listed below.

Genera not Placed

Palaearctic

Genus SCAPTIELLA Enderlein, 1923

Genotype: monotypic for *Pangonia aperta* Loew, 1859, Portugal.

According to Marino (1951), the type ♂ in the Vienna Museum remains unique. It was placed in *Diatomineura* (i.e. eyes hairy, cell R_5 open) by Kröber (1939). It may be a scionine or a pangoniine; perhaps more likely the latter, because it is not separable on present information from the Nearctic *Pilimas*.

Genus CORIZONEURA auct., nec Rondani

Several Palaearctic species have been described as having bare eyes, ocelli, and open cell R_5. At least some have also a short proboscis, large labella, and no appendix to R_4. The great zoogeographical interest of this group has already been indicated, and a list of the species I have been able to find in the available literature is therefore appended: *hispanica* Kröber, 1921, ♀, Spain; *annulata* Bigot, 1892, ♀, southern Europe; *caucasica* Kröber, 1921, ♂♀, Russian Kurdistan; *oritensis* Bigot, 1892, ♂, Caucasus; *bazini* Séguy, 1934, ♂♀, China (described as *Buplex*); *chekiangensis* Ôuchi, 1939, ♂♀, E. China; *enokizonoi* Ôuchi, 1939, ♂, Japan; *yezoensis* Shiraki, 1918, ♀, Japan.

Dr. Fairchild has sent me the following notes on a cotype male of "*C.*" *caucasica* Kröb. in the United States National Museum: "Eyes bare, holoptic, well differentiated and demarcated into large and small facets, the former about two-thirds of eye area. Ocelli prominent. Face not produced; proboscis shorter than head, the labella large and membranous. Subepaulet and *sc* bare; all cells but anal open. Not congeneric with .....*Pangonius.*"

My present impression is that these species will probably be found to belong to Group 1 of Pangoniini.

Nearctic

Genus ZOPHINA Philip, 1954

Genotype: monotypic for *Apatolestes* (or gen. nov.) *eiseni* Townsend, 1895, Lower California.

This little known species may be a chrysopine, or a pangoniine related to *Asaphomyia.*

Neotropical

Genus LEPTOFIDENA Kröber, 1930

Genotype: *Leptofidena beelzebul* Kröber, 1930, Argentina, by original designation.

Eyes hairy, cell R_5 closed. The genotype is described as a slender, rather bare species, with metallic sheen, excavated palpi, and the terminal annulus of the 3rd antennal segment rod-shaped.

Three Ethiopian genera, *Pseudoscaptia* Enderlein, 1922 (described as Melpiinae), *Aphotriclista* Enderlein, 1934, and *Discione* Enderlein, 1934 (both described as Scionini), have been transferred to Chrysopinae on advice from Mr. Oldroyd.

Tribe PANGONIINI (Loew, 1860)

Style of ♂ hypopygium bifid. Gonopophyses of ♀ not widely separated, and distal edge of 8th sternite not strongly chitinized. Ocelli always present; eyes usually bare; callus occasionally developed; 3rd antennal segment with the basal annuli often swollen and sometimes fused.

Wing with cell M_3 always open; vein R_4 nearly always with strong appendix. Species of varied size and appearance.

The tribe can be divided into two fairly well-defined groups of genera.

Group 1.—Cell R_5 open. Proboscis little if at all longer than head height, usually stout; labella distinctly expanded, usually large and soft. Eyes bare or hairy. Face normal or bulging forward in a rounded snout (Fig. 17), rarely conically produced. Species of very varied form, often parallel-sided, occasionally quite slender. Nearctic, Neotropical, Australasian (? Palaearctic).

Group 2.—Cell R_5 nearly always closed. Proboscis of variable length, from about head height to very much longer, nearly always slender; labella nearly always unexpanded, chitinized, sometimes quite long and narrow. Eyes bare. Face normal or conically produced. Mostly stout, *"Pangonia"*-like flies. Palaearctic, Nearctic, Neotropical.

Group 1 is the more primitive in proboscis and wing characters, and it contains the most generalized species, though it also includes some that are specialized in antennal structure or unusual in some other respect. Broadly speaking, the trend in Group 1 is to parallelism with primitive Bouvieromyiini, and in Group 2 to parallelism with more specialized Scionini and Philolichini. A link between the two groups is provided by *Austroplex,* which has many features in common with *Esenbeckia translucens* (compare Figs. 12 and 20*D*).

Presentation of keys to genera will not be attempted in this series. They would necessarily be incomplete, and it would seem better to define the genera I have examined, and offer brief notes on others which appear to be related to them. In any case, the field worker will find regional keys of more practical use.

Group 1
Nearctic

Genus APATOLESTES Williston, 1885

Genotype: originally monotypic for *Apatolestes comastes* Williston, 1885, California.

Species examined.—comastes Will., ♀; *comastes willistoni* Bren., ♂ ♀; *parkeri* Phil., ♂; all det. Philip.

A primitive group of slender-bodied, short-legged species, specialized only in often having a shiny frons, prominent callus, and somewhat swollen palpi in the ♀. The following definition is based on the genotype.

Female

Eyes bare. Ocelli well developed; ocellar tubercle flat. Frons wide (index* less than 2), diverging, shining, with a large, transverse, bulging,

* The *frons index* is here defined as

$$\frac{\text{length from vertex to top of subcallus}}{\text{width at mid-length of frons}}.$$

The width at mid-length usually gives a better indication of the mean breadth of the frons than an index based on measurement at its lower end.

polished callus on its lower part (not developed in all species of the genus). Subcallus small, tomentose; parafacials wide; face rather flat, tomentose, and hairy. Antennae slender; 3rd segment subulate, 8-annulate. Palpi with 1st segment short; 2nd distinctly swollen, hairy, nearly as long as the short, fleshy proboscis; labella large. Hind tibial spurs rather short. Vein R_1 with appendix. Hypopygium: cerci rounded; 8th sternite broad, with well-separated gonopophyses; caudal ends of spermathecal ducts slender, unexpanded, moderately chitinized.

Fig. 6.—*Apatolestes comastes willistoni* Bren.: *A*, *C*, head of ♀; *B*, proboscis and palp of ♂; *D*, ninth tergite and genitalia of ♂; *E*, eighth sternite and terminal segments of ♀. Left-hand scale for *A*, *B*, *C*; right-hand scale for *D*, *E*.

Subsequent figures will have approximately the arrangement shown here. It is to be noted that hairs, the flagella of the ♂, and the spermathecal ducts of the ♀ have been omitted from most of the drawings in this series of papers.

Male

Similar to ♀. Eyes meeting in mid-line; upper facets more or less enlarged and differentiated from the lower. Ocelli prominent, on a large tubercle. Face hollow; face and parafacials very hairy. Second segment of palpi cylindrical, very hairy. Hypopygium without unusual features.

Distribution.—Western United States and south-western Canada.

Genus BRENNANIA Philip, 1941

Nom. nov. for *Comops* Brennan, 1935, nec Aldrich, 1934.

Genotype: monotypic for *Pangonia hera* Osten-Sacken, 1877, California.

Species examined.—hera (O.-S.), ♂ ♀, det. Philip.

Related to *Apatolestes*, from which it is differentiated chiefly by the strongly hairy eyes and hairy body. Its appearance is so different that separation at the generic level seems justified.

Female

Eyes with long, dense hairs, easily visible at ×15. Frons medium (index 2.2), diverging, irregularly grooved longitudinally, and with a large, somewhat shining area on lower two-thirds; ocellar tubercle sunken but prominent. Subcallus small, tomentose, hairy on each side. Parafacials

wide; face sunken; both with long, dense hairs. Antennae: 1st segment short and thick; 2nd small; 3rd wide at base and tapering evenly, 8-annulate. Palpi: 1st segment swollen; 2nd swollen at base, with a deep dorsal concavity, tapering to a rounded point apically; both segments obscured by long hairs. Proboscis very short; labella large and soft.

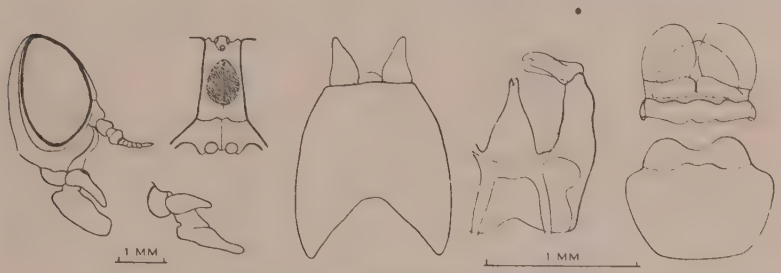


Fig. 7.—*Brennania hera* (O.-S.).

Thorax and abdomen covered with long, rather silky hairs. Legs moderately stout, with long hairs; hind tibial spurs medium. Wing with cell R_5 distinctly narrowed at margin; vein R_4 with long appendix. Genitalia similar to *Apatolestes*.

Male

Similar to ♀, but even more hairy. Eyes meeting in mid-line; upper facets slightly larger than lower. Palpi with 1st segment almost globular, 2nd more conical than in ♀. Cell R_5 not appreciably narrowed at margin; appendix to vein R_4 shorter than in ♀. Hypopygium similar to *Apatolestes*.

Distribution.—California.

Genus PILIMAS Brennan, 1941

Genotype: *Diatomineura californica* Bigot, 1892, California, by original designation (in a footnote to Philip (1941*b*); the genus was described in 1935 without indicated genotype).

Species examined.—californica (Big.), ♂ ♀; *abaureus* (Philip), ♂ ♀; *ruficornis* (Big.), ♂ ♀; all det. Philip.

Usually more robust species than *Apatolestes*, with narrower, entirely tomentose frons, longer proboscis, and more or less hairy eyes.

Female

Eyes with short, fine, inconspicuous hairs. Frons medium (index about 3), slightly diverging, entirely tomentose; subcallus small, tomentose; parafacials narrow above, widening below; face convex. Antennae with base of 3rd segment distinctly swollen and basal 2 or 3 annuli more or less indistinct, showing an approach to the form seen in *Esenbeckia*. Palpi moderately slender, subcylindrical, tapering, nearly as long as shaft of proboscis. Proboscis about equal to head height; labella

well developed. Hind tibial spurs strong. Wing as in *Apatolestes*: vein R_4 with appendix. Hypopygium: gonopophyses large, close together, rounded; caudal ends of spermathecal ducts without expansions, delicate, sometimes difficult to see;* cerci with prominent apical lobe in *californica* and *abaureus*, pointed and fused together in *ruficornis* (Fig. 8A). The whole hypopygium is pale and delicately chitinized in the specimen of this species, and the condition of the cerci may be an abnormality.

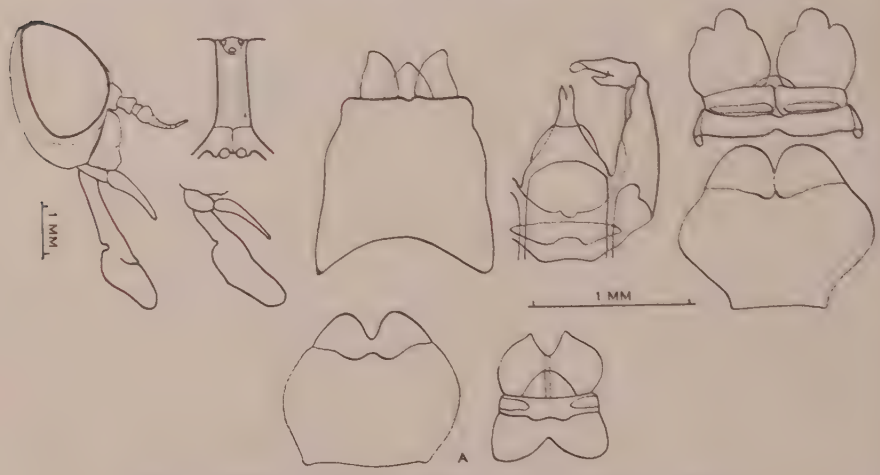


Fig. 8.—*Pilimas californica* (Big.). *A*, *P. ruficornis* (Big.).

Male

Eyes contiguous; upper facets more or less enlarged, but not sharply differentiated; hairs on eyes longer than in ♀, quite dense in *californica*, sparse in *abaureus* and *ruficornis*. Palpi more slender and pointed than in ♀ and more hairy. Hypopygium similar to *Apatolestes*, but aedeagus wider, flagella rather small, and lobes of style longer, the dorsal being prolonged into a finger-like projection.

This genus has a considerable superficial resemblance to *Scaptia*, to which Philip (1941*a*, 1941*b*) has drawn attention.

Distribution.—Western United States and south-western Canada; almost exactly coextensive with that of *Apatolestes*.

Genus STONEMYIA Brennan, 1935

Genotype: *Pangonia tranquilla* Osten-Sacken, 1875, New Hampshire, by original designation.

Species examined.—*tranquilla* (O.-S.), ♂ ♀, det. Philip; *rasa* (Loew), ♂, det. Stone, ♀, det. Bromley.

* The appearances described in this series of papers are those seen in cleared specimens mounted in balsam.

This genus is of special interest, in that it is one of the few in which the principal characters lie in the genitalia. Externally, it differs from *Pilimas* only in having the eyes practically bare in both sexes and vein R_1 without an appendix (the latter seems to be the more reliable character), and one would have doubted whether even subgeneric separation would be justified. The genitalia (Fig. 9), however, are quite distinctive. In the ♂, the aedeagus is unusually wide at the mouth, the flagella are large and

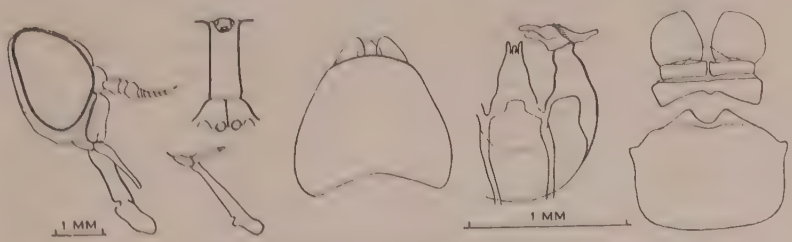


Fig. 9.—*Stonemyia tranquilla* (O.-S.).

strong, and the style has an unusual, outwardly projecting wing. In the ♀, the cerci have no apical lobe, the gonopophyses are relatively small, and the caudal ends of the spermathecal ducts are strongly chitinized and expanded at the ampullar end (Fig. 2*E*). These characters may be of generic value, but it would be wise to leave a final decision on the status of *Stonemyia* and *Pilimas*, until the Palaearctic species of *Scaptiella* and *"Corizoneura"* have been re-examined.

Distribution.—Southern Canada and United States, in a wide band on the east and a narrower one on the west.

Genus ASAPHOMYIA Stone, 1953

Genotype: monotypic for *Asaphomyia texensis* Stone, 1953, Texas.

Species examined.—texensis Stone, ♂ ♀, det. Stone.

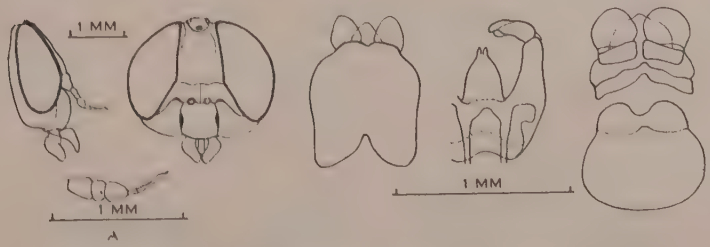


Fig. 10.—*Asaphomyia texensis* Stone. *A*, Antenna of ♀.

This curious, drab little species was described, understandably, as related to *Merycomyia*, but dissection shows it to belong here.

Female

Head an unusual broad oval in face view, considerably flattened in profile. Eyes with short, fine hairs, about as in ♀ of *Pilimas*. Ocellar tubercle prominent and ocelli large. Frons wide (index less than 2), diverging, without callus, and with sparse, short hairs. Subcallus wide, flat, without hairs. Parafacials broad; face somewhat sunken. Antennae remarkably modified, superficially very like *Pseudopangonia* (Chrysopinae); 1st and 2nd segments short; basal section of 3rd short, conical, about same size as 1st segment; terminal portion forming a narrow, 2-annulate style, which in one antenna shows indications of subdivision into a 3rd annulus. Palpi short, plump, soft, hairy. Proboscis very short, with well-developed, soft labella. Legs short and moderately stout; hind tibial spurs well developed. Wing with cell R_4 unusually long, cell R_5 widely open; vein R_4 with appendix. Hypopygium: 9th tergite a broadly V-shaped bar, 10th normal, cerci rounded; 8th sternite with broadly rounded gonopophyses; caudal ends of spermathecal ducts delicate, difficult to see by ordinary transmitted light.

Male

Eyes large, meeting over a considerable distance in mid-line; upper facets markedly enlarged, apparently bare, clearly separated from a small area of lower, distinctly hairy, small facets. Palpi not as stout as in ♀, more evenly tapering. Hypopygium normal for tribe; aedeagus more like that of *Chaetopalpus* than the other Nearctic genera, but style somewhat differently shaped.

Distribution.—Texas.

Neotropical

Genus CHAETOPALPUS Philippi, 1865

Genotype: *Tabanus annulicornis* Philippi, 1865, Chile, by original designation.

Dasyapha Enderlein, 1922. Type *Dasyapha bisulcata* Enderlein, 1925, Chile, by original designation. Synonymy by Kröber, 1932.

Species examined.—*annulicornis* Phil., ♂; *coracinus* (Phil.), ♂ ♀; both det. Philip.

Small, chrysopine-like species, with hairy eyes and a 5-annulate 3rd antennal segment.

Female

Eyes with long, dense hairs. Frons wide (index 2.2), diverging, largely shining, irregularly hollow in middle, and with a median ridge below, which may represent a callus. Subcallus shining above, tomentose below, without hairs; parafacials wide, very hairy; face convex but rather sunken, tomentose, with long hairs at the sides. Antennae with 1st and 2nd segments normal; 3rd expanded basally, and tapering rapidly to a

well-defined, 4-annulate style; the basal section shows only traces of subdivision. Palpi long, subcylindrical, tapering, with long, dense hairs. Proboscis very short, thick, with large, soft labella. Hind tibial spurs small, inconspicuous. Wing normal; R_4 with appendix. Hypopygium similar to *Apatolestes*, but the gonopophyses not as separated, and 9th tergite wider; caudal ends of spermathecal ducts missing.

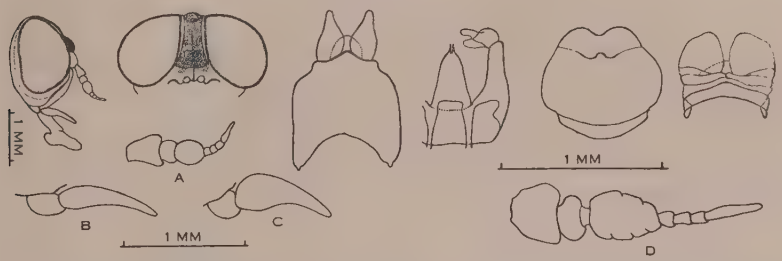


Fig. 11.—*Chaetopalpus coracinus* (Phil.). *A*, Antenna of ♀. *B*, Palp of ♂. *C*, *Chaetopalpus annulicornis* Phil., palp of ♂. *D*, *Histriosilvius longipalpis* (Macq.), antenna of ♀, from drawing of type by Dr. G. B. Fairchild (right-hand scale for genitalia, not for *D*).

Male

Similar to ♀. Eyes meeting in mid-line, upper facets not enlarged. Face hollow. Palpi of *C. coracinus* subcylindrical, of *C. annulicornis* decidedly swollen; very hairy in both species. Hypopygium similar to *Apatolestes* and related genera, but style with a rounded basal swelling.

Distribution.—Central Chile; southern Argentina.

In all essential characters *Chaetopalpus* comes near *Apatolestes*, from which it is differentiated mainly by its hairy eyes, modified 3rd antennal segment, and more compact build. *Asaphomyia* probably represents a separate line of evolution.

The origin of the name is curious, Philippi (1865) merely stating that he had intended to propose *Chaetopalpus* for the group containing *annulicornis*, but decided against it (for reasons which we now know to have been inadequate). It seems, however, to have come into fairly general use.

Genus PROTODASYAPHA Enderlein, 1922

Genotype: originally monotypic for *Tabanus hirtuosus* Philippi, 1865, Chile.

I have not seen this genus, but, from Hack's (1953) figure of the ♂ hypopygium of *P. lugens* (Phil.), it clearly belongs here. It is apparently close to *Chaetopalpus*, differing chiefly in the subulate, 8-annulate 3rd antennal segment, the 1st annulus being only somewhat larger than the others. Described as having hairy eyes, long, hairy palpi, short, fleshy

proboscis, cell R_5 open, and vein R_4 with appendix. Hack's figure shows the style of the ♂ hypopygium as bifid and with a basal swelling like that of *Chaetopalpus*.

Distribution.—Chile; southern Argentina (Neuquén).

The following genera are placed in this tribe tentatively on various suggestive points in their description.

Genus HISTRIOSILVIUS Kröber, 1930

Genotype: monotypic for *Pangonia longipalpis* Macquart, 1847, Brazil.

Described as Silviini. Third antennal segment 5-annulate; eyes bare; cell R_5 open; vein R_4 with appendix. Drawings of Macquart's type in the British Museum made by Dr. Fairchild show the head to be differently shaped from *Chaetopalpus*, but the antennae and palpi (the former reproduced here as Fig. 11*D*) suggest Pangoniini. He noted also that the head is considerably narrower than the thorax; the proboscis short, with long, narrow, membranous, hairy labella; and the abdomen unusually long and slender, the 6th tergite being but little shorter than the 2nd.

Genus PROTOSILVIUS Enderlein, 1922

Genotype: *Protosilvius termitiformis* Enderlein, 1925, Brazil, by original designation.

Third antennal segment 8-annulate; eyes bare; cell R_5 open; vein R_4 with long appendix; slender, yellowish, rather bare species. The description suggests an insect like the Australian *Ectenopsis*.

Australasian

Genus AUSTROPLEX, gen. nov.

Corizoneura auct., pt., nec Rondani, 1863.

Buplex Ferguson and Hill, 1922, p. 248; Ferguson, 1924, p. 256, 1926, p. 294; nec Austen, 1920.

Genotype: *Austroplex goldfinchi*, sp. nov., Queensland, by present designation. (Chosen because specimens of both sexes in good condition are available for study.)

Species included.—*goldfinchi*, sp. nov., ♂ ♀; *chrysophilus* (Walk.), ♀; *brevipalpis* (Macq.), ♂ ♀.

Large, smooth-bodied species, resembling *Esenbeckia*, but differing in having a shorter, stouter proboscis, with well-developed, soft labella, widely open cell R_5, flat, differently shaped callus, and somewhat different ♂ genitalia, which suggest relationships with *Ectenopsis* rather than *Esenbeckia* (compare Figs. 12, 13, and 20).

Female

Eyes bare. Frons of medium width (index about 3), parallel or slightly diverging, tomentose, and with a small, well-defined, elongate callus; ocellar tubercle prominent. Subcallus normal, tomentose, without

hairs; parafacials narrow; face convex. Antennae like those of *Esenbeckia*, with the 3rd segment distinctly expanded basally, normally 8-annulate, with the last annulus long and slender, and usually with the basal annuli rather poorly defined. Palpi long, sabre-shaped or broadened basally, and with a lateral bare area. Proboscis about equal to head height, stout, with large, expanded, unchitinized labella. Hind tibial spurs strong. Wing with cell R_5 widely open; vein R_4 with strong appendix. Hypopygium with gonopophyses conical; caudal ends of spermathecal ducts variable, sometimes delicate, sometimes moderately chitinized.

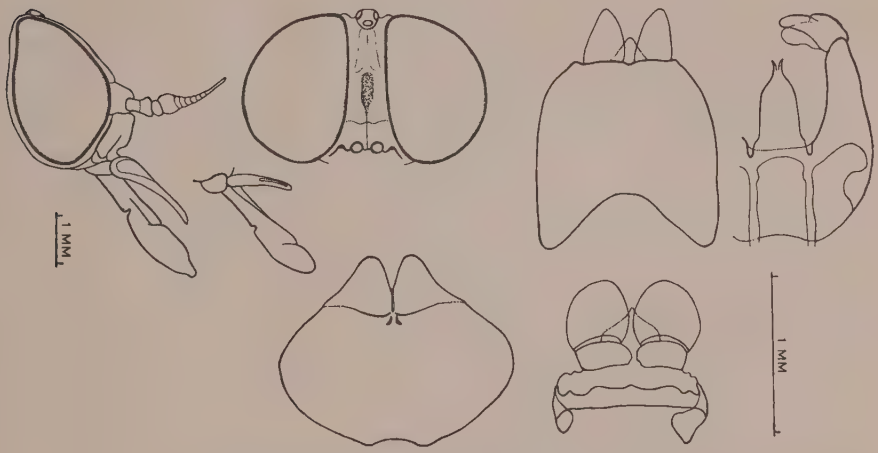


Fig. 12.—*Austroplex goldfinchi*, gen. et sp. nov.

Male

Similar to ♀. Eyes bare, contiguous, upper facets distinctly enlarged and differentiated from the lower. Palpi with the 1st segment swollen, and the 2nd subcylindrical, tapering to a blunt point, more hairy than in the ♀. Hypopygium normal; aedeagus with large flagella; both lobes of style rounded at tip, the dorsal considerably smaller than the ventral.

Distribution.—East coastal Australia from Sydney, New South Wales, to Mackay, north Queensland, with one record from south-western part of Western Australia.

AUSTROPLEX GOLDFINCHI, sp. nov.

Types.—Holotype ♀ and allotype ♂, from Yeppoon, Queensland, 4-7.xi.1924, G. M. Goldfinch, in the School of Public Health and Tropical Medicine, University of Sydney.

I have named this species after my old friend and companion on many collecting trips, the late Gilbert M. Goldfinch.

A large, yellowish fawn species; scutum with dark brown sublateral patches behind suture; abdomen with dark brown basal bands, which are less than half the width of the tergites; wings pale greyish with a hint of yellow; legs uniformly yellow. Length 16-20 mm.

A. chrysophilus (Walk.) is somewhat larger and more robust; it has median and sublateral dark vittae extending almost the full length of the scutum; the wings are more yellow; and the dark abdominal bands are more than half the width of the tergites.

Female

Head: Frons parallel, somewhat wrinkled longitudinally, covered with creamy fawn tomentum, except for a small, elongate, greyish brown callus on its lower half; on either side of the callus there is a small group of very short but strong dark hairs, otherwise the frons is bare. Subcallus concolorous with frons, without hairs. Parafacials similar, with a few pale hairs near lower margin; face slightly darker, with a rather narrow zone of dark brown hairs extending across the middle. Antennae with basal segments creamy, with rich brown hairs; 3rd orange-yellow. Palpi nearly as long as proboscis, creamy, with brown hairs except for the brownish orange bare area. Beard short, light brown to yellowish cream.

Thorax: Scutum yellowish fawn, with dull brownish yellow hairs. The shoulders and anterior margin are paler, almost creamy yellow, and there are indications of a pair of short pale creamy stripes on either side of the median line anteriorly. There is an inconstant, elongate, narrow, dark brown patch in the median line at about level of suture, and a larger, elongate, oval, dark brown patch lateral to the almost invisible dorsocentral lines behind the suture. These areas, the part of the scutum just lateral to them, and the zone in front of the scutellum bear dark brown hairs. Scutellum yellowish fawn, with dull golden hairs. Pleurae yellowish fawn, somewhat variable in colour, and with brownish gold to rich brown hairs.

Legs: Yellow, with dull golden to brownish gold hairs.

Wings: Very faintly tinged with grey, costal cell not appreciably darker than the rest; veins yellowish to light yellowish brown.

Abdomen: Bright yellowish fawn, with a dark brown basal patch on either side of the median line on the 1st tergite, and conspicuous black or blackish brown bands on the remaining tergites; these bands are not more than half the width of the tergite in the median area, but tend to widen slightly laterally. Hairs black on the dark areas and bright golden on the pale parts. Venter similarly marked to the dorsum, but the darker colour is more extensive, and tends to be brown rather than black.

Male

Similar to ♀, but the dark sublateral scutal marking behind the suture is sometimes inconspicuous, and the abdominal bands may be interrupted in the median line.

Distribution.—Queensland: Mackay, A. Marriage; Yeppoon, Nov., Goldfinch; Burpengary, 1904, T. L. Bancroft (Ricardo 1915, as ♂ of *chrysophilus*).

Genera ECTENOPSIS Macquart, 1838 and PARASILVIUS Ferguson, 1921

As represented by their genotypes, these two genera are quite distinct. Typical *Ectenopsis* are slender flies, with bare eyes, 8-annulate 3rd antennal segment, long palpi, and a stout proboscis, with large, soft labella. Typical *Parasilvius* are more broadly built, parallel-sided flies, with finely hairy eyes, 3rd antennal segment with an expanded, more or less fused, basal section and a 4-annulate "style", short palpi, and a slender proboscis, with relatively small, firm labella. The genitalia of the males are similar, except for small differences in the shape of the aedeagus, and the cerci of the females are more truncate apically in *Parasilvius* than in *Ectenopsis*. Ferguson, at the time, was perfectly justified in proposing *Parasilvius* as a new genus.

Since then, species have been collected, which are either intermediate or divergent in some of these characters, and it has become clear that we have, not simply two separate entities, but a group of closely related entities. It seems best to recognize these as subgenera of *Ectenopsis*, although in some instances this may tend to exaggerate their true taxonomic status.

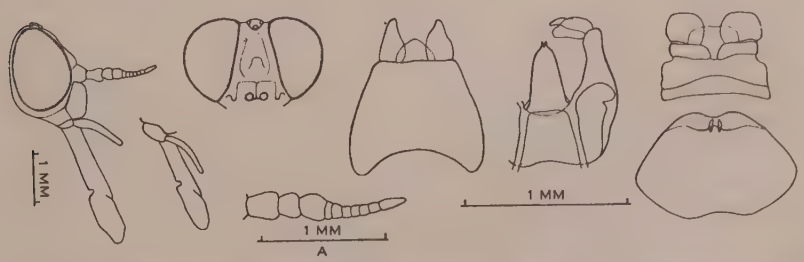


Fig. 13.—*Ectenopsis* (*Ectenopsis*) *vulpecula* (Wied.). *A*, Antenna of ♀.

Subgenus ECTENOPSIS Macquart, 1838

Subgenotype: originally monotypic for *Chrysops vulpecula* Wiedemann, 1828, from unknown country (now known to be Australia).

Species included.—*vulpecula* (Wied.), ♂ ♀; *angusta* (Macq.), ♂ ♀; *australis* Ric., ♂ ♀.

Slender, smooth-bodied, bare-eyed species.

Female

Ocellar tubercle moderately developed. Frons wide (index about 2), diverging, more or less longitudinally furrowed, without callus. Subcallus small, tomentose, without hairs; parafacials narrow; face strongly convex,

but appearing truncate in profile. First and 2nd antennal segments with short hairs; 3rd subulate, clearly 7- or 8-annulate, basal annulus as wide as 2nd segment, and distal annuli not unusually slender. Palpi somewhat flattened, more than half the length of the shaft of the proboscis. Proboscis about equal to head height, stout, with large, soft labella. Vein R_4 with strong appendix. Hind tibial spurs of medium size. Cerci rounded apically; gonopophyses small; caudal ends of spermathecal ducts moderately chitinized, long and slender.

Male

Eyes large, contiguous; upper facets not appreciably enlarged. Third antennal segment a little slenderer than in ♀, and palpi a little shorter. Hypopygium little different from other conservative genera of the group; aedeagus smooth; flagella small-medium; style with dorsal lobe slender, finger-like, ventral lobe swollen.

Distribution.—Eastern coastal Australia, from Moa I. in Torres Strait to Sydney, New South Wales.

Larvae and pupae of *E. angusta* (Fig. 3*A*) were found by English (1953) within a few inches of the surface in black sandy loam near Sydney. The soil was usually moist from soakage, but was well drained and not at all swampy. Some of the larvae were still alive nearly 2 years after they were captured. Adults were taken resting on vegetation in the same area, but they were not observed to feed, either by Miss English or by other workers who have collected them in the field.

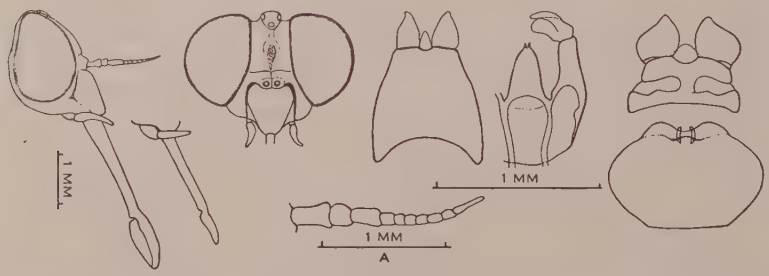


Fig. 14.—*Ectenopsis* (*Leptonopsis*) *vittata*, subgen. et sp. nov. *A*, Antenna of ♀.

Subgenus LEPTONOPSIS, subgen. nov.

Subgenotype: *Ectenopsis* (*Leptonopsis*) *vittata*, sp. nov., Western Australia, by present designation.

Species included.—vittata, sp. nov., ♂ ♀ ; sp. (W. Aust.), ♂.

An exaggerated *Ectenopsis*, but with very slender 3rd antennal segment, triangularly produced face, and the palpi and proboscis of *Parasilvius*.

Eyes bare. Ocellar tubercle of ♀ unusually raised and prominent. Frons of ♀ wide (index less than 2), with a small, central callus. Face strongly produced to form a well-defined triangle in profile. Third antennal segment clearly 8-annulate, very slender, little more than half width of 2nd at base. Palpi very short, awl-shaped. Proboscis relatively long and slender, with relatively small, firm labella. Hind tibial spurs medium.

Distribution.—Western Australia, from Monte Bello I. to Geraldton.

ECTENOPSIS (LEPTONOPSIS) VITTATA, sp. nov.

Types.—Holotype ♀, from Ardingly, Western Australia, 26.x.1953, J. H. Calaby, in the Division of Entomology, C.S.I.R.O., Canberra; allotype ♂, from Monte Bello I., Western Australia, 5.ix.1951, H.M.S. "Campania" collection, in the British Museum (Natural History), London.

A brightly marked, grey species, distinguished from all other members of the genus by having a strongly vittate thorax, and a median brown stripe and lateral brown margins on the abdomen. Legs light creamy brown; wings vaguely darkened along the crossveins. Length 10-12 mm.

Female

Head: Frons covered with pale fawn-grey tomentum; there is a small, longitudinal, light brown callus, and some short dark hairs above the middle on either side. Subcallus, parafacials, and face pale fawn-grey, with rather short, dark hairs on face and lower part of parafacials. Antennae with basal segments yellowish cream, with short black hairs; 3rd unusually long and slender, reddish brown, darkening on apical 4 annuli. Palpi short, light creamy fawn, with white hairs on the basal segment and relatively long but fine black ones on the 2nd segment. Proboscis slightly longer than height of head. Beard ashy white.

Thorax: Scutum with a dark brown, narrow, continuous, median line lying on a lighter brown median area; the dorsocentral lines are strong, widened anteriorly, and ashy grey; and there is a wide ashy grey lateral area, so that the brown sublateral areas are reduced to broad vittae, which are interrupted at the suture, and do not reach the fore or hind margin; there is also a brown lateral spot above the wing root. Hairs fairly long but fine, brown in colour. Scutellum grey laterally, brown in the median area, completing the appearance of a median brown stripe extending from the front of the thorax to the tip of the abdomen. Hairs long, fine, mixed dark brown and greyish white. Pleurae light grey, with greyish white and brown hairs.

Legs: Light fawn, with a little greyish tomentum on the femora. Hairs on femora mixed greyish white and black; black on the tibiae and tarsi.

Wings: Greyish, with brown veins; somewhat suffused with brown anteriorly, and with narrow, rather vague, brownish clouds on *r-m*, the basal section of R_4 proximal to the appendix, the apex of the discal cell, and *m-cu*.

Abdomen: Pale fawn-grey, with a broad brown median stripe, which is narrowly interrupted at the apices of the tergites, and with brown lateral patches on each tergite. Hairs short, mixed black and cream; marginal hairs ashy white, inconspicuous. Venter very pale fawn-grey, with the apices of the sternites pale grey, and with inconspicuous, short, pale hairs.

Male

Similar to ♀, but more hairy, and darker scutal vittae not so complete. Eyes large, contiguous, bare; upper facets distinctly enlarged but not sharply separated from the small lower and lateral facets. Palpi rather shorter than in ♀.

Distribution.—Western Australia: Monte Bello I., Sept., H.M.S. "Campania"; Northampton, Nov., A. J. Turner; Arjana, Oct., Calaby; Ardingly, Oct., Calaby.

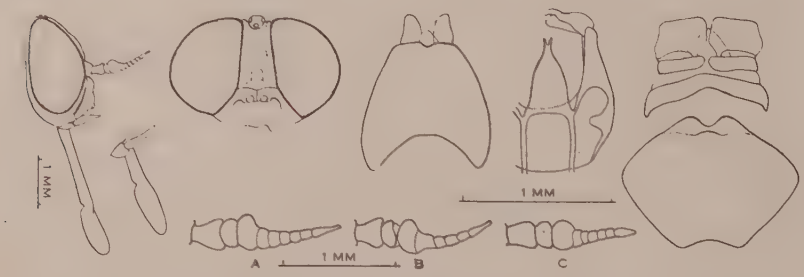


Fig. 15.—*Ectenopsis* (*Parasilvius*) *fulva* (Ferg.). *A*, Antenna of holotype ♀; *B*, of sp. (W.A.) ♀; *C*, of *victoriensis* (Ferg.) ♀.

Subgenus PARASILVIUS Ferguson, 1921

Subgenotype: originally monotypic for *Parasilvius fulvus* Ferguson, 1921, Victoria.

Ommia Enderlein, 1922. Monotypic for *Ommia prisca* Enderlein, 1925 (= *Ectenopsis? victoriensis* Ferguson, 1921), Victoria. Synonymy by Ferguson, 1926.

Species included.—*fulva* (Ferg.), ♂♀; *hamlyni* (Tayl.), ♂; *victoriensis* (Ferg.), ♂♀; sp. (W. Aust.), ♂♀.

Parallel-sided species of medium build. Eyes with short, fine hairs in ♀, usually visible at ×20; longer but sometimes rather sparse hairs in ♂ (much as in *Pilimas*). Ocellar tubercle of ♀ moderately developed. Frons of ♀ usually rather narrower than in *Ectenopsis*, without callus. Face convex. Third antennal segment swollen at base, wider than 2nd; basal 3 or 4 annuli more or less completely fused, apical 4 clearly defined. Palpi very short, usually awl-shaped. Proboscis relatively slender, with relatively small, firm labella. Hind tibial spurs medium. Cerci of ♀ truncate apically.

Reduction of the annuli of the 3rd antennal segment is variable. In *E.* (*P.*) *fulva* and sp. (W. Aust.), the segment is sometimes unequivocally

5-annulate, but more often shows traces of basal annulations as indicated in Figure 15*A*, *B*. *E.* (*P.*) *victoriensis* lies almost midway between *Ectenopsis* and *Parasilvius* in habitus, and in the shape of the 3rd antennal segment, which is usually 6- or 7-annulate (Fig. 15*C*); I have placed it here on account of its perceptibly hairy eyes and short palpi.

Distribution.—South-eastern Queensland; Victoria; South Australia; south-western Western Australia.

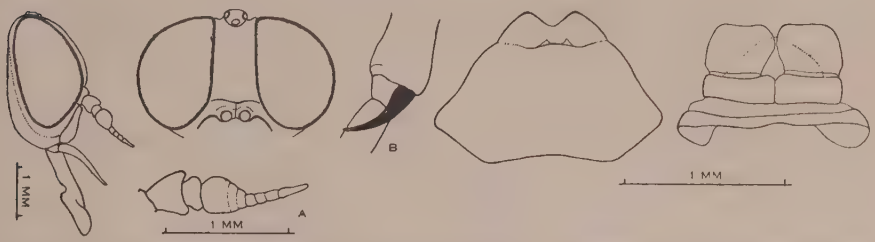


Fig. 16.—*Ectenopsis* (*Paranopsis*) *lutulenta* (Hut.). *A*, Antenna of ♀; *B*, hind tibial spur of ♀.

Subgenus PARANOPSIS, subgen. nov.

Subgenotype: monotypic for *Apatolestes lutulentus* Hutton, 1901, New Zealand.

Species included.—lutulenta (Hutton), ♀.

A robust, though long-bodied, smooth species, with compacted 3rd antennal segment, and very large hind tibial spurs.

Female

Eyes bare. Ocellar tubercle raised and prominent. Frons wide (index 2), without callus. Face convex. Third antennal segment with basal 4 annuli widened and more or less completely fused, apical 4 clearly defined and forming a well-differentiated style. Palpi rather flattened, longer than shaft of proboscis. Proboscis about equal to head height, stout, with large, soft labella. Hind tibial spurs unusually large and powerful (Fig. 16*B*). Cerci as in *Parasilvius*.

Distribution.—North and South Islands of New Zealand.

Genus CAENOPROSOPON Ricardo, 1915

Genotype: originally monotypic for *Caenoprosopon wainwrighti* Ricardo, 1915 (= *Corizoneura trichocera* Bigot, 1892), New South Wales.

Demoplatus Ricardo, 1915. Type *Corizoneura trichocera* Bigot, 1892, Australia, by original designation. Synonymy by Ferguson, 1926. I believe that the respective genotypes are the sexes of one species; *Caenoprosopon* has page priority.

Cryptoplectria Enderlein, 1923. Monotypic for *Demoplatus australis* Ricardo, 1915, New South Wales. Synonymy by Ferguson, 1926. I concur, from examination of the genotype.

Species included.—trichocerus (Big.), ♂ ♀ ; *australis* (Ric.), ♂ ; *nigrovittatus* (Ferg. & Hill), ♂ ; *minor* (Tayl.), ♂.

A curious group, in which the female of only one species but the males of several are known.

In the ♀, *C. trichocerus* is distinguished from *Ectenopsis* by more robust build, projecting, hairy subcallus, strongly bulging face, and very large, sabre-shaped palpi (Fig. 17). The 3rd antennal segment is very slender, and the annuli sometimes reduced to 6 or even 5. The caudal ends of the spermathecal ducts can be seen only by phase-contrast microscopy.

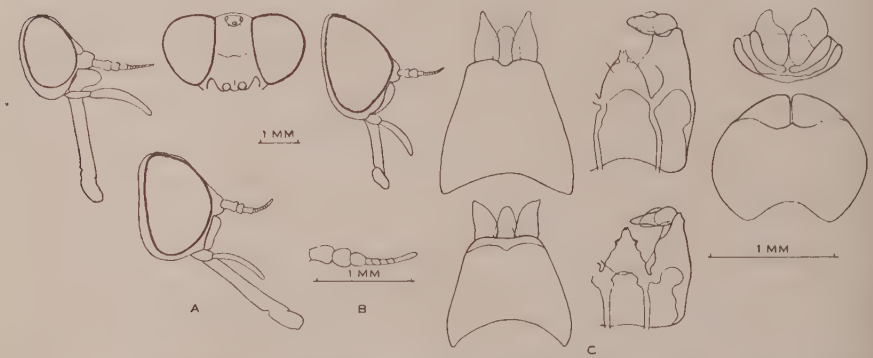


Fig. 17.—*Caenoprosopon trichocerus* (Big.), including lateral view of head of male. *A, C, C. australis* (Ric.) ♂ ; *B,* antenna of *C. minor* (Tayl.) ♂.

The ♂ ♂ fall into two groups: *C. trichocerus,* paler, and with markedly enlarged upper facets on the eyes; and the remaining darker species, which have the facets almost uniform throughout. The palpi are more slender than in the ♀, gently curved, and about as long as the shaft of the proboscis. The face does not project. The hind tibial spurs are small, and tend to disappear. Hypopygium distinguished by the small, broadly triangular aedeagus and exceedingly small flagella; shape of lobes of style also rather distinctive. The name *Cryptoplectria* End. is available, if separation of the group of dark species proves to be necessary when the females are discovered.

Distribution.—East coastal Australia, from Palm I., near Townsville, Queensland, to Sydney, New South Wales.

Genus THEREVOPANGONIA, gen. nov.

Genotype: monotypic for *Therevopangonia insolita,* sp. nov., Western Australia.

Female

Exceedingly small (7-8 mm), parallel-sided, bristly, therevid-like species. Eyes small, very finely hairy. Frons exceedingly wide (index 1),

diverging, tomentose, without central callus, but with a pair of oblique, narrow, shining, bare areas covering the junction with the wide, strongly projecting, otherwise tomentose subcallus. Face somewhat bulbous. Antennae with 1st segment somewhat swollen, a little less than twice as long as broad; 2nd rounded; 3rd wider than 1st and 2nd, swollen basally, and with a short, well-defined style; the basal part is either single or divided into 2 or 3 indefinite annuli, and the style is clearly 3-annulate, so that the whole segment is 4-6-annulate. Palpi short, tapering, rather like *Parasilvius*, hairy. Proboscis about equal in length to head height,

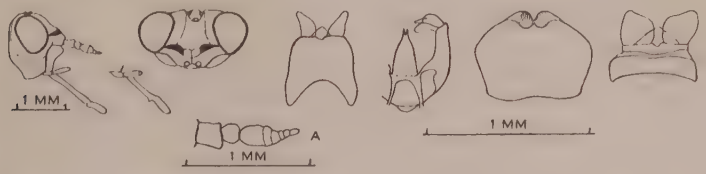


Fig. 18.—*Therevopangonia insolita*, gen. et sp. nov. *A*, Antenna of ♀.

slender; labella small, chitinized. Legs short, stout, bristly; hind tibial spurs well developed. Vein R_4 of wing with appendix; cell R_5 open. The 8th sternite is intermediate in shape between *Ectenopsis* and *Caenoprosopon*, and the 9th tergite is a broad chitinized sclerite.

Male

Similar to ♀, but smaller. Eyes large, contiguous, finely hairy; facets on the upper four-fifths distinctly, though not greatly, enlarged. Subcallus not projecting, and face retreating, unlike that of ♀. Palpi smaller than in ♀. Ninth tergite strongly arched, notched apically; aedeagus smooth; flagella well developed but small; dorsal lobe of style slender, finger-like as in *Ectenopsis*, ventral lobe large.

The outstanding features of the genus are the therevid-like facies, and the quite unusual form of the 3rd antennal segment. The only known species was collected in spring in dry country in Western Australia. Nothing is recorded of its habits or life history.

Therevopangonia insolita, sp. nov.

Types.—Holotype ♀, from Geraldton, Western Australia, 5.ix.1926, and allotype ♂, from Eradu, near Geraldton, 8.ix.1926, E. W. Ferguson, in the School of Public Health and Tropical Medicine, University of Sydney.

A very small, dark greyish to brown species; with short antennae; greyish scutum; stout, grey and yellowish brown, bristly legs; greyish wings, with a well-defined stigma; and dark brown abdomen, with paler apical bands on the tergites. Length: ♀ 7-8 mm, ♂ 5-7 mm.

Female

Head: Frons covered with greyish tomentum, which is a little darker on either side of a central slightly depressed area: the lateral areas with numerous long creamy yellow and brown hairs. Ocellar tubercle prominent, grey, bearing long dark hairs. Subcallus pale creamy grey below the shining brown band on each side. Parafacials wide, pale grey, with long brown and creamy yellow hairs. Face creamy grey, with inconspicuous creamy hairs. Antennae with basal segments light brownish grey, with long black hairs: 3rd yellowish brown at extreme base, remainder dark brown. Palpi short, subcylindrical, pale brownish grey, with very long brown and creamy hairs. Proboscis deep greyish brown. Beard creamy, long but sparse.

Thorax: Scutum dark grey, with indefinite lighter grey dorsocentral lines, pale grey shoulders, and grey lateral margins. Hairs long, relatively dense, black or dark brown, rather conspicuous on presutural lateral area. Scutellum grey, with fine black hairs. Pleurae grey, with long dull creamy hairs.

Legs: Short and stout, femora, especially the hind ones, distinctly swollen. Coxae and femora greyish brown, with long, dull creamy and black hairs. Tibiae and tarsi yellowish brown, fore and mid with mixed bristly black and golden hairs, the hind a little darker than the others and with golden hairs.

Wings: Grey; stigma dark brown, conspicuous.

Abdomen: First tergite light grey, with brownish lateral patches and pale creamy grey apical margin; remaining tergites dark brown, with pale greyish fawn apical margins. Hairs not very conspicuous, brown on the darker parts, yellowish cream on the paler areas and lateral margins. Venter light grey, with pale greyish cream hairs and some black ones near apex of abdomen.

Male

Similar to ♀, but smaller and even more hairy. The head is wide, but the subcallus and face do not project as in the ♀. The abdominal markings are variable, some specimens being like the ♀, while in others the grey colour predominates, the brown being reduced to form darker basal bands, sometimes interrupted in the median line, on tergites 2–4.

Distribution.—Western Australia: Geraldton and Eradu, Sept., Ferguson, Nicholson; Dongarra, Sept.-Oct., R. E. Turner (Brit. Mus.).

Group 2

This group includes three genera, which intergrade to some extent, and are therefore more conveniently dealt with serially than by separate zoogeographical regions. Of the three, *Pangonius* is Palaearctic, *Esenbeckia* is Neotropical and southern Nearctic, and *Proboscoides* is Neotropical.

Genus PANGONIUS Latreille, 1802

Genotype: *Tabanus proboscideus* Fabricius, 1794 (= *Tabanus mauretanus* Linnaeus, 1764), Mediterranean, by designation of Latreille, 1810 (*teste* Coquillett, 1910).

Tanyglossa Meigen, 1804. Monotypic for *Tabanus haustellatus* Fabricius, 1781, Europe, *teste* Coquillett, 1910 ("1 species. Type *Tabanus mauretanus* Linnaeus (as *haustellatus* Fabricius)"). Synonymy by Coquillett, 1910. *P. haustellatus* is not now regarded as a synonym of *P. mauretanus* (see below).

Tacina Walker, 1850. Type *Pangonia micans* Meigen, 1820, southern Europe, by designation of Coquillett, 1910. Synonymy by Surcouf, 1921.

Pangonia Rondani, 1863. Clearly a *lapsus*, as he refers throughout to *Pangonia* Latrielle. This variant has no standing, but gained wide currency for many years.

Dasysilvius Enderlein, 1922. Monotypic for *Pangonia variegata* Fabricius, 1805, southern Europe. Considered a synonym of *Mesomyia* by Enderlein (1925), but Oldroyd (personal communication) has pointed out that it is quite an ordinary "*Pangonia*", and listed as such by Séguy (1926) and Kröber (1939).

Taeniopangonia Szilàdy, 1923. Defined, without included species. Kröber (1925) included six species, from which I now select* the first, *proboscideus* Fabricius, 1794, as subgenotype, the name thus becoming an absolute synonym of *Pangonius*.

Melanopangonia Szilàdy, 1923. Defined, without included species. Kröber (1925) included four species, from which I now select* the second, *marginatus* Fabricius, 1805 (= *haustellatus* Fabricius, 1781) as subgenotype, the name becoming an absolute synonym of *Tanyglossa* Meig.

?*Ectinocerella* Séguy, 1929. Type *Pangonius* (*Ectinocerella*) *surcoufi* Séguy, 1929, North Africa, by original designation. Status uncertain.

Species examined.—*mauretanus* (Linn.), ♂, det. Kröber as *proboscideus* Fabr.; *mauretanus* var. *aethiops* (Szil.), ♀, det. Philip; *haustellatus* (Fabr.), ♂, det. Szilàdy as *marginatus* Fabr., ♀, det. Philip; *micans* Meig., ♀, det. Oldroyd.

As this is the type genus of the subfamily, the characters of its genotype may be defined in some detail.

A medium-sized species, with rounded body, triangularly produced face, long, slender proboscis, unexpanded labella, and unusually long, thin legs.

Female

Eyes bare. Ocelli well developed. Frons wide (index about 2), diverging, tomentose, without callus. Subcallus normal, tomentose, without hairs; face swollen and triangularly produced. Antennae subulate; 3rd segment 8-annulate, its basal annulus longer than wide and about as wide as 2nd segment, 8th annulus not markedly elongate. Palpi very short; 1st segment distinctly longer than the 2nd, which is acorn-shaped, and has a small but deep dorsolateral apical concavity. Proboscis slender, about two and a half times head height, with unexpanded, inconspicuous labella. Legs long, unusually slender, with well-developed hind tibial spurs. Wing

* I cannot discover in the literature available to me that types have been designated for these two names.

with cell R_5 closed, cell M_3 open; vein R_1 with well-developed appendix. Hypopygium: gonopophyses rounded distally and approximated to one another; cerci rounded apically; caudal ends of spermathecal ducts delicate, unexpanded tubes, which are not easily seen by ordinary transmitted light.

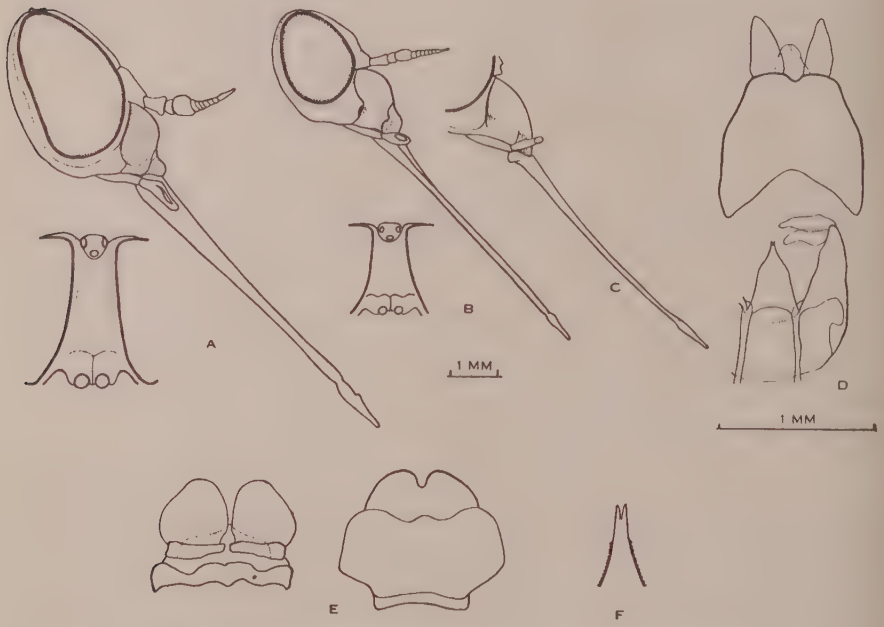


Fig. 19.—*A*, *Pangonius haustellatus* (Fabr.) ♀; *B-E*, *P. mauretanus* (Linn.) ♂ and var. *aethiops* (Szil.) ♀; *F*, part of aedeagus of *P. haustellatus*, showing serrations at higher magnification.

Male

Similar in general characteristics to ♀. Eyes contiguous, upper facets slightly enlarged; antennae more slender than in ♀; palpi more truncate, and with an apical dorsolateral bare area. Hypopygium: aedeagus with fine lateral serrations on its apical half (visible at × 100); flagella well developed, strongly chitinized; style bifid, both limbs bluntly pointed.

P. haustellatus differs from *mauretanus* in being more robust, with stronger legs, and in having a somewhat narrower frons (index 2.5), the basal annulus of the 3rd antennal segment considerably larger, the terminal annulus longer, the face bulging but not triangularly produced, the proboscis about twice the head height, the 2nd segment of the palpi slightly longer and similar in the sexes, the cerci of the ♀ truncate apically, and the style of the ♂ larger and its limbs more pointed.

Kröber (1939), following Szilàdy (1923) and Séguy (1929), recognized the equivalent of four subgenera in *Pangonius*. Of these, *Pangonia* Szil. nec Rond., is feebly differentiated, lacks a name, and does not seem to be worthy of recognition. The status of *Ectinocerella* cannot be assessed from the description; it could possibly be a philolichine. This leaves two, which, to judge by their type species, may possibly prove worthy of recognition as subgenera, namely, *Pangonius* (syns. *Dasysilvius*, *Taeniopangonia*) and *Tanyglossa* (syns. *Tacina*, *Melanopangonia*). It is impossible to say more on available information.

Distribution.—Palaearctic: northern Mediterranean; southern Germany, Central Europe, Turkey, Ukraine, Crimea, Georgia; Morocco, Algeria, Tunisia; Asia Minor, Syria; and one somewhat doubtful record (*sinensis* Enderlein, 1932) from China.

Genus ESENBECKIA Rondani, 1863

Dyspangonia Lutz, 1905. Type *Pangonia fuscipennis* Wiedemann, 1828, Brazil, by designation of Bequaert, 1924. Synonymy by Lutz, 1909.

Ricardoa Enderlein, 1922. Type *Pangonia semiflava* Wiedemann, 1830, Mexico, by original designation. Fairchild (1951) doubted the validity of this genus; I concur.

Scapacis Enderlein, 1922. Monotypic for *Scapacis fidenodes* Enderlein, 1925, Mexico. Dr. Philip has informed me that he has seen Enderlein's type, and noted it as probably a synonym of *Esenbeckia saussurei* (Bellardi, 1859) from Mexico. The open, though narrowed, cell R_5 is presumably an aberration.

Genotype: *Silvius vulpes* Wiedemann, 1828, Brazil, by original designation.

Species examined.—Nearctic: *incisuralis* (Say), ♂ ♀; *incisuralis tinkhami* Philip, ♂ ♀; both det. Philip. Neotropical: *semiflava* (Wied.), ♀, det. Philip; *seminuda* (Coq.), ♂ ♀, det. Oldroyd; *wiedemanni* (Bell.), ♀, det. Fairchild; *yepocapa* Fchld., ♂ ♀, det. Fairchild; *vulpes* (Wied.), ♀, det. Fairchild; *prasiniventris* (Macq.), ♂ ♀, det. Oldroyd and Fairchild; *translucens* (Macq.), ♀, det. Philip.

Female

Eyes bare. Frons narrow (index 4 to 5), slightly diverging, tomentose, with or without an elongate, keel-like callus. Subcallus moderately projecting, more or less tomentose, without hairs; face moderately bulging, more or less lightly tomentose. Antennae with 3rd segment distinctly swollen at base, and tapering to an unusually long and narrow apical annulus; there is a tendency for the basal annuli to fuse, and the 3rd segment is often distinctly 7-annulate. Palpi and proboscis variable. Wing with cell R_5 almost always closed, cell M_3 widely open or slightly narrowed; vein R_4 with appendix. Hypopygium of normal form for the group; cerci obliquely truncate apically; caudal ends of spermathecal ducts delicate, usually not detectable by ordinary transmitted light.

Male

Similar to ♀. Eyes large, contiguous; upper facets more or less slightly enlarged, but not sharply differentiated from lower. Hypopygium

similar to *Pangonius*, but the aedeagus is smooth, and the base of the style tends to develop into a rounded bulge or an incipient lateral wing reminiscent of *Stonemyia*.

Distribution.—Neotropical: There appear to be two major centres of radiation, Brazil and Mexico, with fewer species in the intervening countries and on the western side of the continent, and none in southern Argentina and Chile. Nearctic: States adjoining Mexico and north to Kansas.

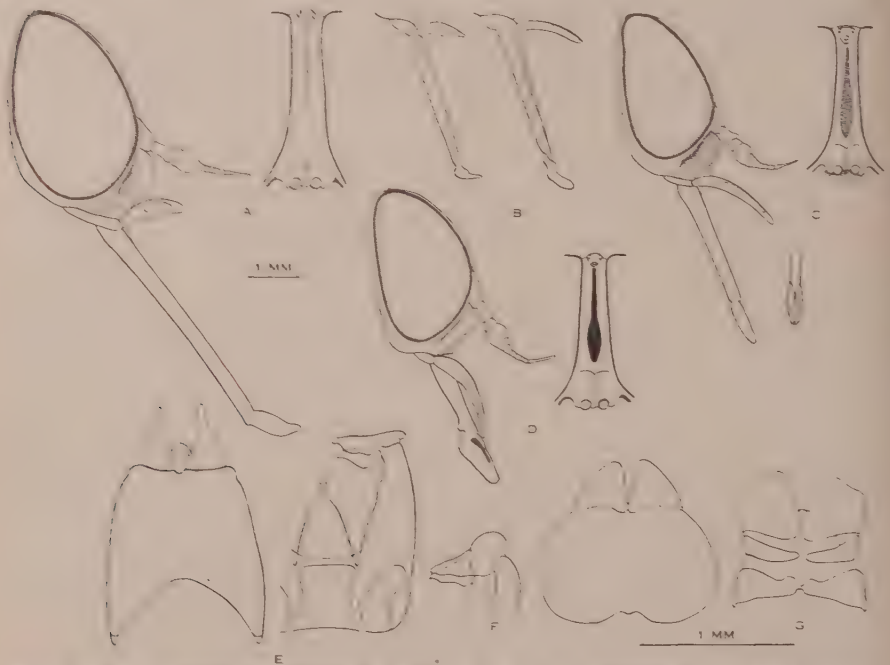


Fig. 20.—A, *Esenbeckia seminuda* (Coq.) ♀; *B*, *E. incisuralis tinklami* Philip, proboscis and palp of ♀ (left) and ♂ (right); *C*, *E. prasiniventris* (Macq.) ♀, including labella from front; *D*, *E. translucens* (Macq.), ♀; *E*, ♂ genitalia of *E. yepocapa* Fchld.; *F*, style of ♂ *E. seminuda*; *G*, ♀ genitalia of *E. wiedemanni* (Bell.).

The species examined may be arranged in a series of progressively increasing specialization in shape of proboscis and palpi and in general robustness of build.

translucens: A relatively long-bodied species, somewhat like a *Tabanus* in shape. Callus well developed. Proboscis about equal to head height, of medium thickness, dull; labella expanded, firm, and only partly chitinized. Palpi as long as shaft, sabre-shaped, rounded at tip, with an extensive, slightly hollow, lateral bare area. A most interesting species, which is only distinguishable from *Austroplex* (Group 1) by the closed cell R_5, better developed callus, and shape of the palpi.

prasiniventris: Slightly more compactly built. Callus well developed. Proboscis about equal to head height, moderately slender, shining; labella chitinized, unexpanded, elongate, distinctly forceps-like, leading to the specialization seen in *Proboscoides*. Palpi about three-fourths length of shaft, of similar form to *translucens*.

vulpes: My specimen of the genotype has lost the labella, and is not in good enough condition for illustration. It is a large, parallel-sided, fawn insect, with brown wings, superficially rather like the Australian *Austroplex brevipalpis*. The frons is without a callus, the palpi like those of *translucens* and *prasiniventris*, and the proboscis moderately slender.

yepocapa and *wiedemanni*: Stoutly built. Callus well developed, but rather dull in *yepocapa*. Proboscis about equal to head height, slender, shining; labella small, unexpanded, chitinized. Palpi nearly as long as shaft, similar to preceding but tapering to a point apically (transition to the following).

incisuralis and *incisuralis tinkhami*: Stoutly built. At most trace of callus. Proboscis a little longer than head height, slender, shining; labella small, unexpanded, chitinized. Palpi slightly less than half the length of the shaft, moderately slender, widened in middle, tapering apically, and with a deep lateral concavity. The palp of *tinkhami* is like that of *Scaptia maculiventris* (Fig. 28*D*).

semiflava and *seminuda* (*Ricardoa* group): Robust, stoutly built species. At most trace of callus. Proboscis about one and a half times head height, slender, shining; labella small, unexpanded, chitinized. Palpi much less than half the length of the shaft; 2nd segment shorter than 1st, but of "*maculiventris*" rather than "*Pangonius*" form, though these species do provide a transition to *P. haustellatus*.

In the males examined (*seminuda, incisuralis, tinkhami, yepocapa*, and *prasiniventris*), the characters of the proboscis correspond to those of the females, but the palpi are relatively uniform, being slender, a little less than half the length of the shaft, more or less flattened apically, and with a more or less well-developed lateral bare area.

The origins of *Esenbeckia* are obscure. Its more primitive members show indications of affinity with both the Australian *Austroplex* and the Nearctic *Stonemyia-Pilimas* complex. They certainly developed from Group 1 ancestors, but whether of southern or northern origin is impossible to say. At the other end of the scale, the specialized *Ricardoa* group leads directly to the *haustellatus* (*Tanyglossa*) group of *Pangonius*. The differences between them are small, and it may prove necessary, when the Palaearctic fauna has been re-examined, to amalgamate the genera but retain a series of subgenera distributed between the three regions. In any case, it is evident that the Palaearctic fauna was derived from the Neotropical, and that a pathway of migration to permit this must have existed in the past.

Genus PROBOSCOIDES Philip, 1943

Genotype: *Proboscoides fairchildi* Philip, 1943, Peru, by original designation.

Species examined.—*fairchildi* Philip, ♂ ♀, det. Philip.

This genus is an offshoot from *Eschatoba*, from which it is distinguished primarily by the heavily chitinized proboscis, with unusually elongate, separate, forceps-like labella (Fig. 21). There is a well-developed callus, and the terminalia of both sexes are like those of *Eschatoba*, except that the 9th tergite of the ♂ is very deeply excavated basally. Subgeneric status might indicate its position better than as a full genus.

Distribution.—Neotropical: Peru, Bolivia, Brazil.

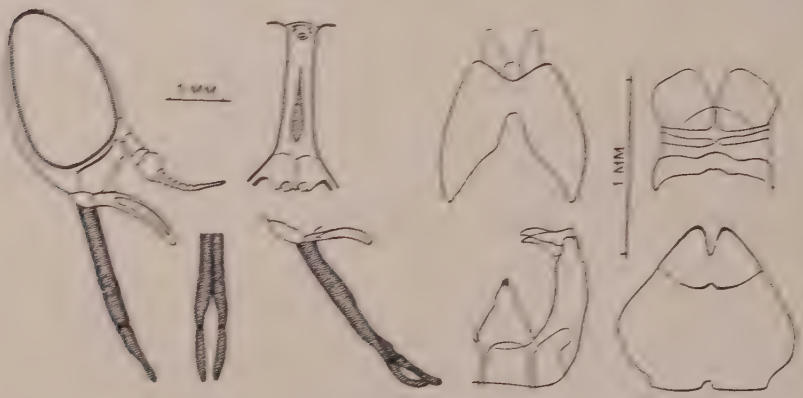


Fig. 21.—*Proboscoides fairchildi* Philip.

Tribe SCIONINI Enderlein, 1922

Style of ♂ hypopygium simple, usually finger-like, sometimes pointed. Anterior gonopophyses of ♀ rounded or conical, approximated to one another, and only moderately chitinized. Eyes nearly always hairy. Ocelli well developed. Face normal to strongly protuberant. Palpi nearly always flattened, and usually with a bare lateral concavity. Proboscis ranging from stout and less than head height to slender and longer than whole body, and labella from large and soft to small and chitinized. Cell R_5 often, and cell M_1 sometimes, closed; appendix on vein R_4 variable, usually absent, short or inconstant. Usually stoutly built, rather hairy flies.

This tribe contains two aberrant, bare-eyed genera, and a considerable number of hairy-eyed forms which can be arranged in a continuous evolutionary sequence. By proceeding down the grade, from the aberrant and specialized to the more generalized, it will be possible to retain a convenient arrangement by zoogeographical regions, without unduly obscuring the evolutionary and systematic problems that have to be discussed.

Nearctic

Genus GONIOPS Aldrich, 1892

Genotype: monotypic for *Goniops hippoboscoides* Aldrich, 1892 (= *Pangonia chrysocoma* Osten-Sacken, 1875), Pennsylvania.

Species examined.—*chrysocoma* (O.-S.), ♂ ♀, det. Philip.

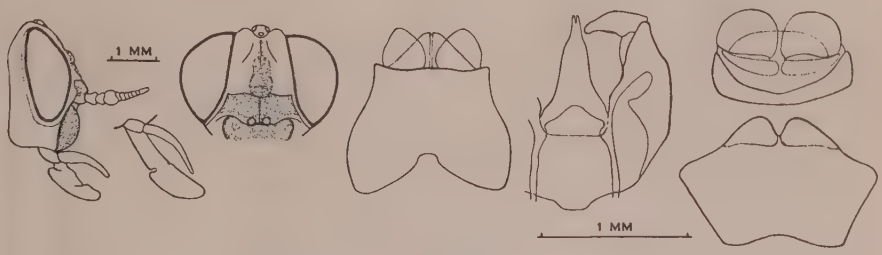


Fig. 22.—*Goniops chrysocoma* (O.-S.).

This curious fly is the only Nearctic representative of the tribe. It has no near relatives, and can be recognized immediately by its broad, rather flat body, small head, and wing pattern.

Eyes bare. Frons of ♀ wide, diverging, shining on lower part; subcallus and face shining. Palpi of primitive form, long, subcylindrical, tapering, hairy, more slender in ♂ than in ♀. Proboscis short; labella large, fleshy. Wings with cells R_5 and M_3 open; vein R_4 without appendix. ♂ and ♀ genitalia without distinguishing features.

The unusual biology of this species has been reviewed by Marchand (1920). The females are not known to suck blood. They deposit their eggs on the undersides of leaves, and brood over them for several days. On hatching, the larvae drop to the ground and apparently live in the soil and debris under the bushes. The flask-shaped form of the larva is curious, but structurally it and the pupa conform to the type later established for *Scaptia*.

Distribution.—Eastern United States, from New York to Arkansas.

Neotropical

Genus MYCTEROMYIA Philippi, 1865

Genotype: originally monotypic for *Pangonia conica* Bigot, 1857, Chile.

Silvestriellus Brèthes, 1910. Monotypic for *Silvestriellus patagonicus* Brèthes, 1910, Patagonia. Synonymy by Enderlein, 1925.

Caenopangonia Kröber, 1930. Monotypic for *Diatomineura hirtipalpis* Bigot, 1892, Chile. Synonymy by Fairchild (personal communication) from examination of the type of the genotype.

Species examined.—conica (Big.), ♂♀, det. Philip by comparison with type.

Very aberrant, with longer body than is usual in tribe, but wide, rather flat abdomen, projecting face, long, slender proboscis, and long wings. The ♂ has widely dichoptic eyes, a large, bulbous hypopygium, and somewhat resembles an apiocerid.

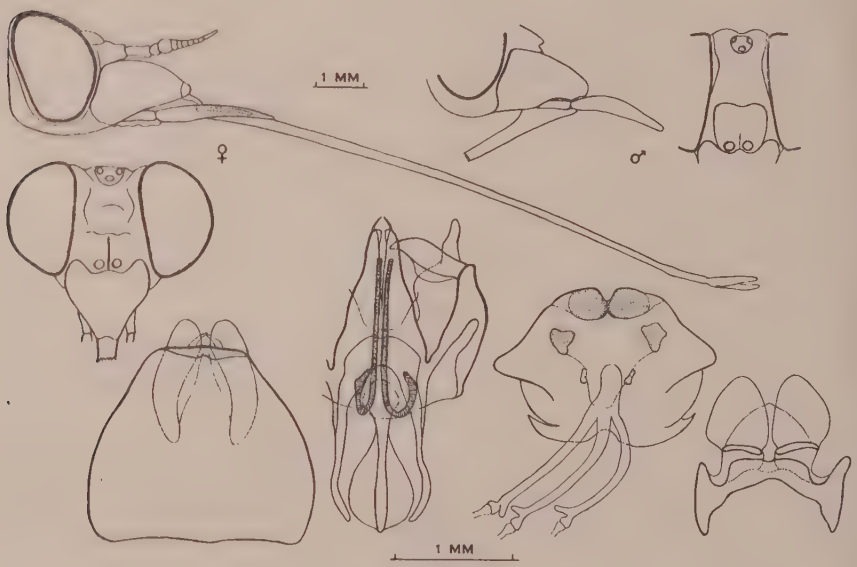


Fig. 23.—*Mycteromyia conica* (Big.).

Female

Eyes with short, sparse hairs, appearing bare at lower magnifications. Ocellar tubercle moderately developed. Frons very wide (index 1.2), irregularly grooved, tomentose, without callus. Subcallus markedly projecting, hairy at sides; parafacials narrow; face produced conically. Antennae: 1st segment slender, nearly twice as long as wide; 2nd short; 3rd subulate, 8-annulate, basal annulus not much wider than 2nd segment. Palpi: 1st segment slender; 2nd about three times as long as 1st, sabre-shaped, rounded apically, with a narrow dorsolateral bare concavity. Proboscis about two-thirds length of the whole body, slender, with unexpanded labella. Wings with cell R_5 closed, rather long-petiolate, cell M_3 widely open; vein R_4 angulate, with strong appendix. Legs longer and more slender than usual in tribe, especially fore pair; hind tibial spurs long. Hypopygium unusually large, and remarkable in many ways; 8th sternite broad; gonopophyses small and dark; 9th tergite bilobed; cerci rounded apically; basal section of genital fork small and pale, except for

two short, moderately chitinized bars; caudal ends of spermathecal ducts wide, for the most part lightly chitinized, and each with a conspicuous blind diverticulum (Fig. 23).

Male

Similar to ♀ to a remarkable degree. Ocellar tubercle more prominent; frons wide (index less than 1.5); subcallus and face as in ♀, but hairs on subcallus long; antennae as in ♀, but more slender; palpi as in ♀, but dorsolateral concavity narrower and more obscure. Hypopygium: 9th tergite strongly arched and shield-like, more like that of related primitive families than of normal Pangoniinae; the down-turned distal edge has 2 pairs of pointed projections; aedeagus large and strong, widely open distally; flagella remarkably stout and heavily chitinized; coxites wide and short, and drawn into a finger-like apical projection ventrally; style strongly curved, pointed; the median muscle strut is widened, like a lacrosse racquet.

The genitalia of both sexes are so remarkable as almost to justify removing this genus to a separate tribe, but the structure of the head and proboscis is not unlike that of *Fidena*, and the style of the ♂ hypopygium also indicates affinities with Scionini.

Distribution.—Southern Chile and southern Argentina (Neuquén, Patagonia); also recorded from Brazil (Matto Grosso), but the status of this species is uncertain.

All the remaining genera of the tribe have quite densely hairy eyes (with the single exception of the female of *Scaptia conspicua*), a smooth, tomentose, parallel or diverging frons of medium width, and usually plump, hairy or tomentose bodies.

Genus PITYOCERA Giglio-Tos, 1896

Genotype: monotypic for *Pityocera festae* Giglio-Tos, 1896, Panama.

Species examined.—*festae* G.-T., ♀, det. Fairchild.

This genus is close to *Fidena*, but its antennae (Fig. 24) are so remarkable that separation at the generic rather than subgeneric level is clearly justified. The relatively long-petiolate cell R_{2+3}, on which Kröber (1932) relied to distinguish the Pityocerini, is of more doubtful value. The projecting, shining face and slender palpi are exactly similar to *Fidena*, and there is nothing distinctive in the ♀ hypopygium.

Distribution.—Panama.

There appear to be three ways in which cell R_2 becomes closed. The commonest in all tribes is by simple fusion from the tip. The second is indicated by the curvature of M_1 in *Pityocera* (Fig. 24) and the presence of a stump vein on it in *Elaphella*, suggesting that closure of the cell is by means of a radio-medial cross vein with atrophy of the distal part of M_1. The reverse appears to have occurred in African *Stenophara* (Fig. 36),

vein R_5 being strongly curved and bearing the stump. These different methods are of phylogenetic interest, but little practical value, because the kind of closure is often not clearly indicated.

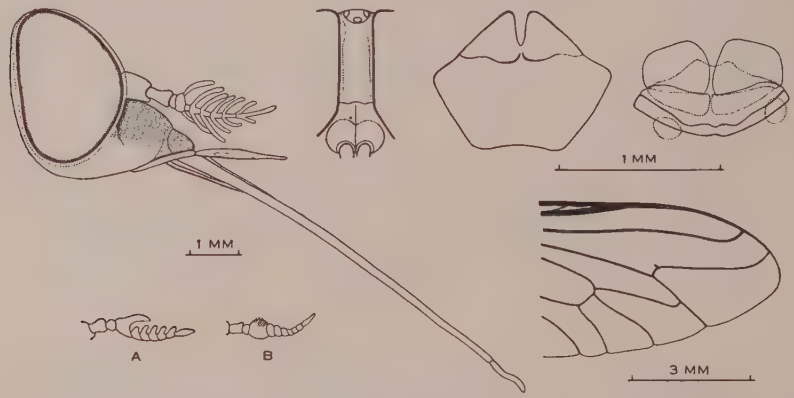


Fig. 24.—*Pityocera festae* G.-T. *A*, antenna of *Elaphella cervus* (Wied.), ♀. *B*, of *Fidena patellicornis* (Kröb.), ♀.

Genus ELAPHELLA Bezzi, 1913

Nom. nov. for *Dicrania* Macquart, 1834, nec Lepeletier and Serville, 1828.

Genotype: monotypic for *Pangonia cervus* Wiedemann, 1828, Brazil.

Diplocus Blanchard, 1845.
Dicranomyia Hunter, 1900, nec Stephens, 1829.
Allodicrania Enderlein, 1913.
Stichocera Hine, 1920.

All these names were proposed to replace Macquart's preoccupied name. *Diplocus* should have priority, but it was overlooked for more than a hundred years, and application has been made by Philip and others (including the writer) for the well-known name *Elaphella* to be conserved.

Species examined.—cervus (Wied.), ♀, det. Fairchild.

Very close to *Pityocera,* in appearance as well as structurally, but the 3rd antennal segment has projections on the dorsal surface only (Fig. 24*A*). Subgeneric separation would indicate the relationships adequately, but it would be an unduly cumbersome arrangement for only two species.

Distribution.—Surinam, Brazil, Peru.

Genus SCIONE Walker, 1850

Genotype: originally monotypic for *Pangonia incompleta* Macquart, 1845, South America.

Diclisa Schiner, 1867. Monotypic for *Pangonia incompleta* Macquart, 1845, South America.

Rhinotriclista Enderlein, 1922. Type *Diclisa maculipennis* Schiner, 1868, Colombia, by original designation. Synonymy by Kröber, 1932.

Species examined.—*incompleta* (Macq.), ♀, det. Philip by comparison with type; sp. nr. *maculipennis* (Schin.), ♀; *aurulans* (Wied.), ♀; both det. Fairchild; ?*fulva* Ric., ♂, det. Philip.

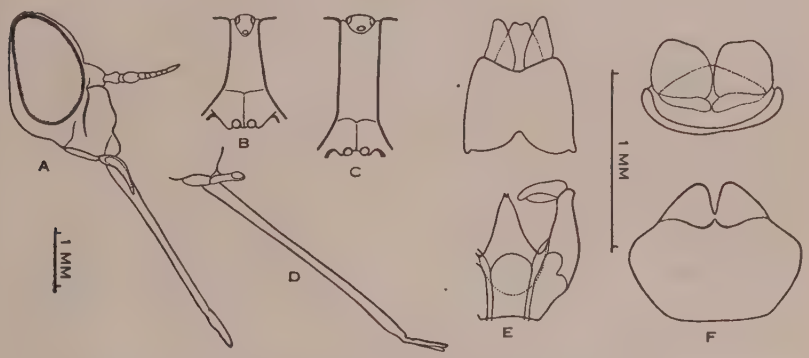


Fig. 25.—*A, B, Scione incompleta* (Macq.) ♀; *C, F,* sp. nr. *S. maculipennis* (Schin.) ♀; *D, E, S. ?fulva* Ric. ♂.

This genus is closely related to *Fidena,* from which it is differentiated primarily by having both cells R_5 and M_3 closed. The frons is parallel or diverging, palpi small and leaf-like as in some species of *Fidena,* and proboscis long and slender, with unexpanded, chitinized labella. On the other hand, there are indications of affinity with the *Pseudoscione-Scaptia* complex in habitus, moderately projecting, tomentose face, and the shape of the 8th sternite of the ♀. There is nothing distinctive in the ♂ hypopygium.

The venational characters appear to be constant in the region, and the group, which includes about 30 species, seems to be a compact, natural one. The genus has considerable local utility, and may therefore be allowed to stand alone, although perhaps the more logical action might have been to include *Fidena* in it as a subgenus.

Distribution.—Mexico, Guatemala, Panama, Colombia, Ecuador, Peru, Bolivia, Venezuela, Brazil, Argentina.

Genus FIDENA Walker, 1850

Genotype: *Pangonia leucopogon* Wiedemann, 1828, Brazil, by designation of Coquillett, 1910.

Melpia Walker, 1850. Type *Pangonia fulvithorax* Wiedemann, 1811, Brazil, by designation of Coquillett, 1910. Synonymy suggested by Kröber, 1930*b*, 1932; I concur from examination of genotype. *Fidena* has page priority.

Erephopsis Rondani, 1863. Type *Pangonia fulvithorax* Wiedemann, 1811, Brazil, by designation of Coquillett, 1910.

Sackenimyia Bigot, 1879. Type *Pangonia fulvithorax* Wiedemann, 1811, Brazil, by designation of Enderlein, 1925.

Phaeoneura Lutz, 1909. Monotypic for *Pangonia basilaris* Wiedemann, 1828, Brazil. Synonymy by Enderlein, 1925.

?*Bombylopsis* Lutz, 1909. Type *Mycteromyia nitens* Bigot, 1892, Brazil, by designation of Fairchild, 1950, on grounds that *Mycteromyia erythronotata* Bigot, 1892, designated by Borgmeier, 1933, was not an originally included species. Synonymy by Kröber, 1934, based on *erythronotata*, but *nitens* apparently belongs here also.

Epipsila Lutz, 1909. Type *Epipsila eriomeroides* Lutz, 1909, Brazil, by designation of Enderlein, 1925. Synonymy by Enderlein, 1925.

Ionopsis Lutz, 1909. Type *Mycteromyia nitens* Bigot, 1892, Brazil, by designation of Enderlein, 1925.

Neopangonia Lutz, 1909. Monotypic for *Neopangonia pusilla* Lutz, 1909, Brazil. Synonymy by Enderlein, 1925.

Bombylomyia Lutz, 1911. Type *Mycteromyia nitens* Bigot, 1892, Brazil, by designation of Fairchild, 1950.

Bombylomorpha Lutz, 1911. Type *Mycteromyia nitens* Bigot, 1892, Brazil, by designation of Fairchild, 1950.

?*Laphriomyia* Lutz, 1911. Monotypic for *Laphriomyia mirabilis* Lutz, 1911, Brazil. Not distinguishable from description.

Micropangonia Lutz, 1922. Type *Neopangonia pusilla* Lutz, 1909, Brazil, by designation of Fairchild, 1950.

?*Pseudelaphella* Kröber, 1930. Type *Pangonia nana* Walker, 1850, Brazil, by original designation. I have not seen the genotype, but *patellicornis* Kröb. is distinguished only by a 3rd antennal segment of rather unusual shape, with a group of black hairs near its base (Fig. 24*B*), and a venation like *Pityocera* and *Elaphella*. Fairchild (1942*a*) regarded it as a link between *Elaphella* and *Fidena*. I agree, but can see no good reason to separate it generically from the latter.

?*Lilaeina* Borgmeier, 1934. Type *Pangonia albifrons* Macquart, 1938, Chile, by original designation. I can find nothing in the description, nor in notes on the ♀ kindly sent me by Dr. Fairchild, to distinguish this genus from *Fidena*.

?*Chrysochiton* Lutz and Castro, 1926. Type *Erephopsis auricinctus* Lutz and Neiva, 1909, Brazil, by original designation. Not distinguishable from description.

Species examined.—beskii (Wied.), ♂; *schildi* (Hine), ♀; *nigripes* (v. Röd.), ♀; *trapidoi* Fchld., ♀; *patellicornis* (Kröb.), ♀; all det. Fairchild; *sorbens* (Wied.), ♂ ♀, det. Philip; *erythronotata* (Big.), ♀, det. Oldroyd; *fulvithorax* (Wied.), ♂ ♀, det. Brit. Mus.

This is the central member of the specialized Neotropical radiation, and the largest, with about 90 species, so it may be described in some detail.

Stoutly built, hairy or tomentose species, with long, slender proboscis, unexpanded labella, and slender palpi.

Female

Eyes with dense hairs. Frons of moderate width (index 2 to 3), parallel to slightly diverging, tomentose, without callus. Subcallus moderately projecting, tomentose, without hairs; face conically produced (Fig. 26) and more or less shining. Third antennal segment subulate, 8-annulate. Palpi very slender; 1st segment almost full length of the projecting snout; 2nd about equal to the 1st, or a little shorter, flattened,

slender, tapering to a fine point, and with a lateral bare area or concavity which is often rotated dorsally. Proboscis projecting forward, longer than head and thorax together, sometimes longer than whole body, with narrow transverse ridges giving it a finely and closely annulate appearance on its whole length; labella long and narrow, chitinized, not at all expanded.* Wing with cell R_5 usually closed or narrowed; cell M_3 widely open; vein R_1 with or without short appendix. Hypopygium without distinctive

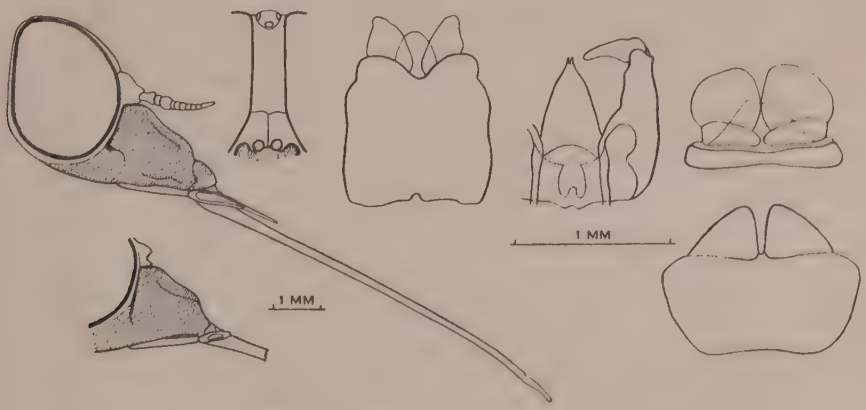


Fig. 26.—*Fidena sorbens* (Wied.).

characters; gonopophyses large and rounded; cerci rather truncate apically; caudal ends of spermathecal ducts slender, simple, moderately chitinized tubes, which can easily be seen by ordinary transmitted light.

Male

Similar to ♀. Eyes large, very densely hairy, contiguous; upper facets at most slightly enlarged in species examined. Hypopygium without distinctive features.

Distribution.—Mexico, Costa Rica, Panama, Colombia; Ecuador, Peru, Bolivia, northern and central Chile; Venezuela, Surinam, Brazil, Paraguay, Uruguay, northern Argentina.

The condition of cell R_5 is obviously of little value, even in the small amount of material I have seen, and I am sceptical about the degree of hairiness of femora and tibiae as generic characters. It might nevertheless be possible, as Fairchild (1941) has suggested, to divide this relatively

* Fairchild has called my attention to the fact that the labium in *Fidena* can be coiled within the head-capsule to bring the shorter piercing parts into action, whereas in Oriental *Philoliche* it is bent aside for this purpose (p. 504). This character may be of considerable phylogenetic importance, but I have not been able to use it satisfactorily for ordinary systematic purposes.

large genus into natural groups which could be given subgeneric status, in which case some of the names listed above would be available for the appropriate segregates.

Neotropical-Ethiopian-Australasian

Genus SCAPTIA Walker, 1850

The remaining species of the tribe are best treated as belonging to a single genus, *Scaptia,* which may be divided into six reasonably distinguishable subgenera. In the absence of males of certain South American species, this arrangement is to some extent tentative.

Scaptia merges into *Fidena,* via the subgenus *Pseudoscione,* the most useful points of distinction being: face nearly always tomentose and less strongly projecting; proboscis less than twice head height (in South American species), not unusually slender; labella clearly defined, usually expanded, never very long and narrow; 2nd segment of palp usually longer than 1st, and not narrowly leaf-like. Although it is difficult to define a precise point of division between the series, the great majority of species can be so readily placed that separation at the generic level is both convenient and reasonable.

The subgenera fall into two groups on genitalic characters:

Style of ♂ finger-like, rounded at tip; cerci of ♀ usually truncate apically: *Scaptia, Pseudoscione, Pseudomelpia.*

Style of ♂ hooked, pointed at tip; cerci of ♀ usually rounded apically: *Myioscaptia, Plinthina, Palimmecomyia.*

The genitalia of the first group are similar to those of *Fidena* and *Scione*; but the style of the ♂ in the second group has proved useful in resolving some of the confusion, which Ferguson (1926) found in the relative lengths of proboscis and palpi. His two major groups in the Australian fauna, one with short proboscis and long palpi and the other with long proboscis and short palpi, were marred by two groups of species with short proboscis and short palpi. Both of these have been found to have pointed styles, and Taylor's genus *Palimmecomyia* falls in naturally with them.

Subgenus SCAPTIA Walker, 1850

Subgenotype: *Pangonia aurata* Macquart, 1838, Australia, by designation of Coquillett, 1910.

Osca Walker, 1850. Type *Pangonia depressa* Macquart, 1837 (= *Tabanus latus* Guèrin, 1832), Chile, by designation of Coquillett, 1910. This synonymy was established by Ferguson (1926) and accepted by Bequaert (1930), but Kröber (1932, 1934) and others have continued to use *Osca* for South American species. I have re-examined the genotypes, and consider that they cannot be separated even subgenerically, though they do belong to separate, intergrading groups of species within the subgenus.

Diatomineura Rondani, 1863. Type *Pangonia depressa* Macquart, 1837 (= *Tabanus latus* Guèrin, 1832), Chile, by designation of Coquillett, 1910.

Apocampta Schiner, 1868. Monotypic for *Apocampta nigra* Schiner, 1868 (= *Pangonia subcana* Walker, 1848), Australia. Synonymy by Ferguson, 1926; I concur, from re-examination of both sexes.

Triclista Enderlein, 1922. Monotypic for *Pangonia limbinevris* Enderlein, 1922, nec Macquart, 1855 (= *Pangonia singularis* Macquart, 1845), Australia. Synonymy by Ferguson, 1926; I concur, from re-examination of both sexes.

Bombomimetes Enderlein, 1922. Monotypic for *Pangonia rufoaurea* Philippi, 1865 (= *Pangonia rufa* Macquart, 1838), Chile. Synonymy by Kröber, 1930b; I concur from re-examination of both sexes.

?*Calliosca* Enderlein, 1925. Monotypic for *Calliosca schoenemanni* Enderlein, 1925 (= *Diabasis varia* Walker, 1848), Chile. I can find nothing in the description, nor in notes on the ♂ kindly sent me by Dr. Fairchild, to separate this genus from *Scaptia* in the restricted sense.

Species examined.—Neotropical: *lata* (Guèr.), ♂ ♀, det. Philip and Kröber; *collaris* (Phil.), ♂, det. Philip; *rufa* (Macq.), ♂ ♀, det. Philip and Pechuman. Australian: *aurata* (Macq.), ♀, and 24 other spp. (♂ ♂ of 15, ♀ ♀ of 23).

Female

Frons parallel or even slightly converging. Face truncate. Proboscis normally not longer than height of head, stout, with large, usually soft, labella. Palpi normally more than half the length of the shaft of the proboscis, often as long as shaft, usually laterally compressed. Cerci usually obliquely truncate apically.

Male

Palpi slender, cylindrical, obliquely truncate at tip. Style of hypopygium finger-like, rounded at tip.

Distribution.—South America (8 spp.): Chile, Argentina, Bolivia, Peru. Australia (25 spp.): eastern coastal and highlands from north Queensland to Tasmania; South Australia; south-western Western Australia.

The species fall into three main groups: the *guttata* group of four, large, robust Australian species, with cell R_5 (and sometimes M_3) closed; the *aurata* group of 17 medium sized to small Australian species, with cells R_5 and M_3 open, though R_5 is occasionally narrowed; and the *lata* group of eight South American and four Australian species, which is intermediate between the other two.

All the anomalous species known to me belong to the *aurata* group. Some specimens of *S. subcana* have a slightly diverging frons, but the proboscis is short and stout, and the palpi are long. Four species (*plana* (Walk.), *tricolor* (Walk.), most specimens of *ruficornis* (Macq.) and a few of *pulchra* (Ric.)) have palpi which do not reach the middle of the proboscis, and in *ruficornis* the proboscis is often rather longer than the head height, while in *tricolor* the labella are quite small and firm. They can all, however, be distinguished from Australian *Pseudoscione* by their parallel frons and the shape of their palpi, and from *Myioscaptia* and *Plinthina* by their palpi, colour pattern, and open cell R_5.

Larvae and pupae of *Scaptia auriflua* (Don.), which is closely related to the subgenotype, were found by Fuller (1936) in damp soil in the mountainous country of southern New South Wales. They occurred near the surface, often among grass roots, and did not invade the wet soil of the swamps. The larvae fed readily on larvae of Tipulidae, which were

Fig. 27.—*Scaptia*, subgen. *Scaptia*. Top row: *S. singularis* (Macq.), Australia (*guttata* group). Middle, *S. lata* (Guér.), Chile. Bottom row: *S. aurata* (Macq.) ♀, and *S. patula* (Walk.) ♂, Australia; *A*, eighth sternite of *S. patula* ♀.

abundant in the area, but they were not cannibalistic. The evidence suggested that the duration of the life cycle was 2, or possibly 3 years. Morphologically, both larvae and pupae (Fig. 3*B*) showed evident relationships with those of *Goniops*.

Subgenus PSEUDOSCIONE Lutz, Araujo & Fonseca, 1918

Subgenotype: *Diatomineura longipennis* Ricardo, 1902, Brazil, by designation of Fairchild, 1950.

Clanis Walker, 1850, nec Hübner, 1816. Type *Pangonia contigua* Walker, 1848 (= *Pangonia lasiophthalma* Macquart, 1834), Australia, by designation of Coquillett, 1910. Preoccupied.

Copidapha Enderlein, 1922. Monotypic for *Copidapha bifasciata* Enderlein, 1925 (= *Corizoneura conspicua* Ricardo, 1915), North Queensland. Reduced to synonym of *Scaptia* (s.l.) by Ferguson, 1926; I concur, from re-examination of both sexes.

Listriosca Enderlein, 1922. Originally monotypic for *Pangonia australis* Enderlein, 1922, nec Philippi, 1865 (renamed *Listriosca flavipes* Enderlein, 1929), Chile. Fairchild informs me that *longipennis* (Ric.) agrees quite closely with species that have been placed in *Listriosca*, and Kröber (1934), who apparently missed the earlier *Pseudoscione*, included *longipennis* in *Listriosca* in his catalogue. There is little doubt that the two names apply to the same concept.

Listrapha Enderlein, 1922. Type *Pangonia latipalpis* Macquart, 1850, Chile, by original designation. I cannot find characters to separate the ♀ of the genotype from *Pseudoscione*.

Parosca Enderlein, 1922. Type *Pangonia viridiventris* Macquart, 1838, Chile, by original designation. Reduced to synonym of *Listrapha* by Kröber, 1932; I concur, from examination of ♀.

Astypia Enderlein, 1925. Type *Pangonia jacksonii* Macquart, 1838 (= *Pangonia maculiventris* Westwood, 1835), Australia, by original designation. Reduced to synonym of *Scaptia* (s.l.) by Ferguson, 1926; I concur, from examination of both sexes.

Listraphella Enderlein, 1929. Type *Listraphella schoenemanni* Enderlein, 1929, Chile, by original designation. This genus appears to be separated from *Pseudoscione* only by having a short appendix to R_4, a character of no value in the present group.

Species examined.—South America: *australis* (Phil.) (*Listriosca*), ♀, det. Fairchild; *viridiventris* (Macq.) (*Parosca*), ♀, det. Fairchild; *latipalpis* (Macq.) (*Listrapha*), ♀, det. Philip. South Africa: *barbata* (Linn.), ♀, det. Oldroyd. Australia: 21 spp. (♂♂ of 12, ♀♀ of 21). New Guinea: *taylori* Oldr., ♀, det. Oldroyd. New Zealand: 5 spp. (♂♀ of all).

Female

Frons distinctly diverging, often markedly so. Face truncate to strongly projecting. Proboscis moderately slender, usually considerably longer than height of head, with relatively small, firm labella. Palpi rarely reaching beyond mid-length of shaft, usually much shorter, of variable form, but usually with well-defined lateral concavity. Wing with cell R_5 open or closed, cell M_3 open. Cerci usually truncate apically.

Male

Palpi variable, nearly always stout with a subapical concavity in Australian species, more slender and tapering in New Zealand species. Style of hypopygium finger-like, rounded at tip.

Distribution.—South America (18 spp.): Chile, Argentina, Peru, Brazil, Venezuela. Africa (3 spp.): South Africa, ? Senegal. Australia (21 spp.): eastern coastal and highlands from northern Queensland to Victoria; one record from Tasmania; South Australia; south-western Western Australia. New Guinea (12 spp.). New Zealand (5 spp.): North and South Islands.

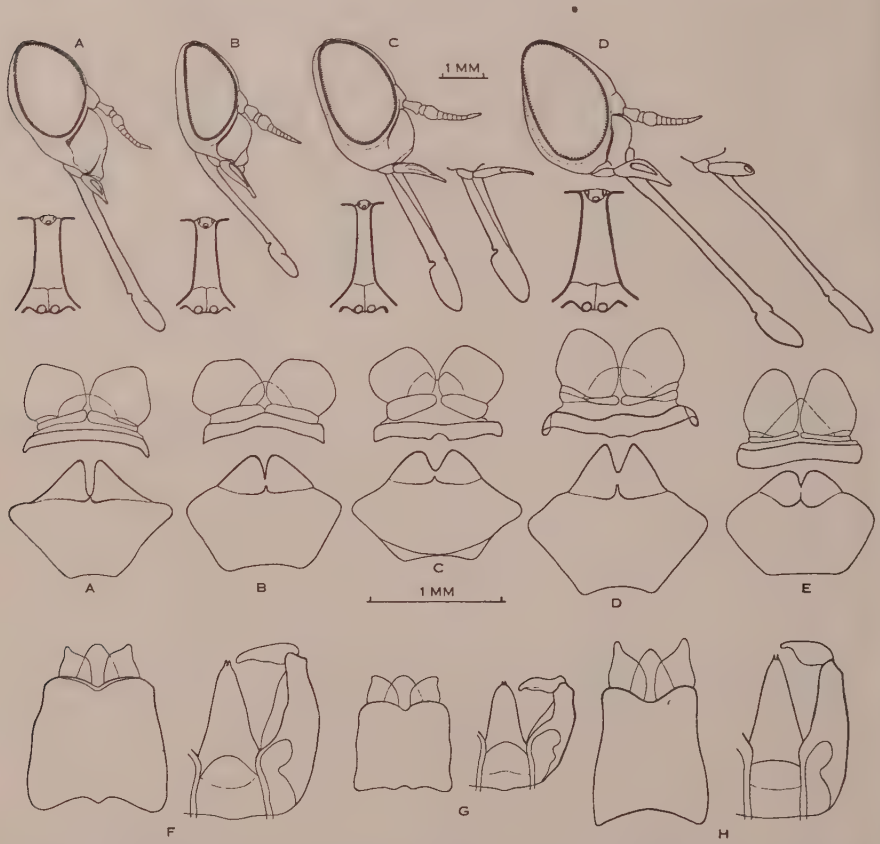


Fig. 28.—*Scaptia*, subgen. *Pseudoscione*. Heads and ♀ genitalia of: *A*, *S. australis* (Phil.), Chile; *B*, *S. latipalpis* (Macq.), Chile; *C*, *S. lerda* (Walk.), New Zealand; *D*, *S. maculiventris* (Westw.), Australia (last two including proboscis and palp of ♂). *E*, ♀ genitalia of *S. barbata* (Linn.), South Africa (for head see Part I, Fig. 7*b*). ♂ genitalia of: *F*, *S. lerda*; *G*, *S. maculiventris*; *H*, *S. vicina* (Tayl.), Australia.

The species from different countries have evolved some distinctive features during their undoubtedly long period of isolation in widely separated parts of the world. Those from South America have a narrower frons, more projecting face, shorter proboscis and more variable palpi than

the Australian species. *S. viridiventris* would be difficult, if it occurred in Australia, in that it provides a link between *Pseudoscione* and the *aurata* group of *Scaptia,* but the two subgenera seem to be well differentiated in South America.

The Australian species mostly have a wide, markedly diverging frons, truncate to moderately bulging face, the proboscis at least one and a half times the head height, and the palpi unequivocally shorter than half the shaft and of distinctive form in both sexes (Fig. 28*D*).

The South African and New Guinea species examined conform to the Australian type, but the New Zealand species are more like their South American relatives. The face does not project so much, but the frons is relatively narrow, the proboscis not much longer than the head height, and the palpi flattened. *S. montana* (Hut.)* is unusual. It is small, dark, rotund, and looks like a *Myioscaptia,* but the style of the male hypopygium is rounded at the tip.

The name *Copidapha* End. is available, if the species with truncate face prove to require separation from those with a projecting snout, when the males of the latter come to be examined.

Early stages of *S.* (*Pseudoscione*) *vicina* (Tayl.) have been described by English (1955). Only two larvae were found, one in soil on a steep slope, and the other under a raked-up heap of decaying leaves and grass. The situation was drier than that favoured by *S. auriflua,* but morphologically the larvae and pupae of the two species were very similar, as were also those of *S.* (*Myioscaptia*) *muscula* Eng. noted below, so it does not seem likely that characters of subgeneric value will be found in the immature stages of this group.

Subgenus PSEUDOMELPIA Enderlein, 1922

Subgenotype: monotypic for *Pseudomelpia horrens* Enderlein, 1925, Chile (described as Silviinae).

Species examined.—horrens End., ♂ ♀, det. Philip.

Like a small, dark, hairy *Pseudoscione,* but distinguished by the short, thick proboscis, and unusual antennae, palpi, and genitalia.

Female

Frons wide (index about 2), diverging. Antennae with 1st segment swollen, with very long hairs; 2nd normal; 3rd with the basal 4 annuli more or less fused and indistinct, so that the segment may appear superficially to be 5-annulate. Face truncate. Proboscis shorter than height of head, with large, soft labella. Palpi as long as the shaft, swollen. Wing with cell R_5 open. Eighth sternite of unusual shape, with very small, weak gonopophyses (Fig. 29); genital fork large and conspicuous; 9th tergite strong, 10th weak; cerci only slightly flattened apically.

* The eyes are so distinctly hairy in the type ♀ that it is difficult to know how this species came to be described as *"Corizoneura"*.

Male

Palpi unusually long, moderately slender and tapering, with long hairs. Style of hypopygium rounded; aedeagus strongly chitinized, and of rather unusual form.

Distribution.—Chile.

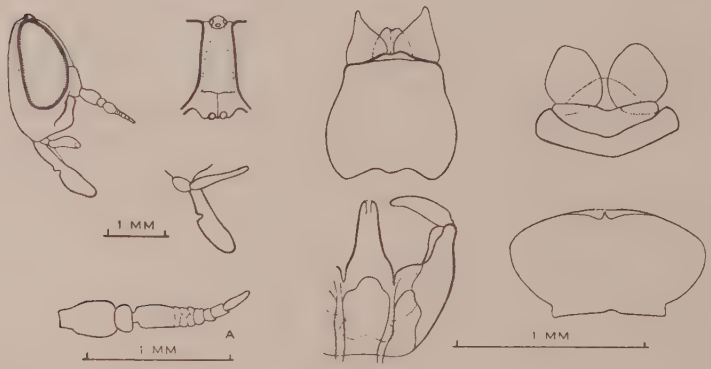


Fig. 29.—*Scaptia* (*Pseudomelpia*) *horrens* (End.). *A*, Antenna of ♂ (cleared preparation).

Pseudomelpia is little more than an aberrant *Pseudoscione*, but it is convenient to treat it provisionally as a distinct subgenus. An undescribed Australian species has several features in common with *Pseudomelpia*, including the short, fleshy proboscis and the large, hairy, 1st antennal segment. The 3rd antennal segment and genitalia are, however, normal, and it probably represents a separate offshoot from the Australian *Pseudoscione* stock.

Subgenus MYIOSCAPTIA, subgen. nov.

Subgenotype: *Pangonia violacea* Macquart, 1850, Australia, by present designation.

Species included.—*violacea* (Macq.), ♂ ♀; *bancrofti* (Aust.), ♂ ♀; *gibbula* (Walk.), ♂ ♀; *muscula* English, ♂ ♀; and 3 undescribed spp. (♂ ♂ of 2, ♀ ♀ of 3).

Small (8-10 mm), rounded bodied, muscoid-like species, with clear wings, and usually bright metallic green to duller semi-metallic black abdomen.

Female

Frons of medium width (index 2.5 to 3.5), parallel or slightly diverging. Face moderately bulging. Proboscis less than one and a quarter times head height, usually slender, with relatively small, firm labella. Palpi very short, flattened, usually broadly leaf-like in lateral view. Wings

with prominent stigma; cell R_5 narrowed, or closed and short-petiolate; cell M_3 open. Cerci rounded apically.

Male

Palpi slender, as in subgenus *Scaptia*. Hypopygium with aedeagus unusually long (Fig. 30); coxites normal; style distinctly hooked and pointed at tip, without strong hairs.

Fig. 30.—*Scaptia* (*Myioscaptia*) *violacea* (Macq.).

Distribution.—Australia: eastern coastal and highlands from north Queensland to southern New South Wales; one species from south-western Western Australia.

The habitus is distinctive, even in the two non-metallic species, and it is interesting that some of the species, although blood-suckers, not only look like blowflies, but behave like them in the note they emit and the apparently aimless irregularity of their flight. They show, in fact, distinct indications of mimicry (Nicholson 1927). Larvae of one of the non-metallic species (*S. muscula* Eng.) have been found in the zone occupied by ant-lion larvae in dry sand on the floor of overhung ledges and small caves in sandstone cliffs (English 1955).

Subgenus PLINTHINA Walker, 1850

Subgenotype: originally monotypic for *Pangonia macroporum* Macquart, 1838 (= *Pangonia binotata* Latrielle, 1811), Kangaroo I.

Species included.—binotata (Latr.), ♀; *divisa* (Walk.), ♀; *cinerea* (Ric.), ♀; *clelandi* (Ferg.), ♂ ♀; *vertebrata* (Big.), ♂ ♀; and 3 undescribed spp. (♂ of 1, ♀ ♀ of 3).

Medium-sized (10-14 mm) species, of normal habitus and tomentose patterns, but with wings usually distinctively marbled, the centres of the cells being darker than along the veins.

Female

Frons medium (index 2.5 to 3), parallel to slightly diverging. Face moderately projecting but truncate. Proboscis less than one and a quarter

times the head height, moderately slender, with relatively small, firm labella. Palpi very short; 2nd segment little, if at all, longer than 1st, thick, rounded apically, and with a large lateral concavity. Wing with cell R_5 closed and often long-petiolate; cell M_3 open. Cerci rounded apically.

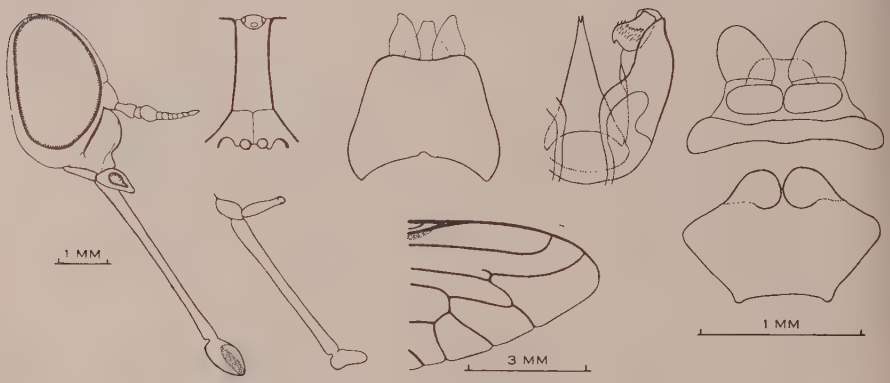


Fig. 31.—*Scaptia* (*Plinthina*) *clelandi* (Ferg.).

Male

Palpi as in subgenus *Scaptia* or rather stouter. Hypopygium (Fig. 31) with aedeagus long; coxite thick and often ridged; style thick, strongly hooked, and pointed at tip, and with a zone of conspicuous, short, thick hairs about middle.

Distribution.—Australia: south-western Western Australia; South Australia and Kangaroo I.; New South Wales and southern Queensland west of the Dividing Range; two species in the eastern coastal zone between Rockhampton and Sydney.

Ferguson (1924, 1926) recognized this subgenus, mainly on the characters of the palpi and wings, and these are now supported by the distinctive features of the male genitalia. *S. vertebrata* differs from the others in having perfectly clear wings, but it agrees well in other respects. Most of the species are found in semi-arid country, and the group seems to have evolved in the west and spread eastwards, in contradistinction to the other subgenera, which appear to have developed in eastern New South Wales and radiated north, south, and westward.

Subgenus PALIMMECOMYIA Taylor, 1917

Subgenotype: originally monotypic for *Palimmecomyia celaenospila* Taylor, 1917 (= *Pangonia walkeri* Newman, 1856), south Queensland.

Species included.—walkeri (Newm.), ♂ ♀; sp., ♀.

Rather long (13-17 mm), narrow, parallel-sided species, with peculiar, waxy integument, and flavid, brown tipped wings.

Female

Frons slightly diverging, with a rudimentary callus in *walkeri*; subcallus more projecting than in other subgenera. Face protuberant, *shining*. Proboscis and palpi as in *Pseudoscione*. Wing with cell R_5 closed or open; cell M_3 open. Cerci rounded apically.

Male

Palpi as in subgenus *Plinthina*. Hypopygium with aedeagus and coxite normal (Fig. 32); style hooked and pointed at tip.

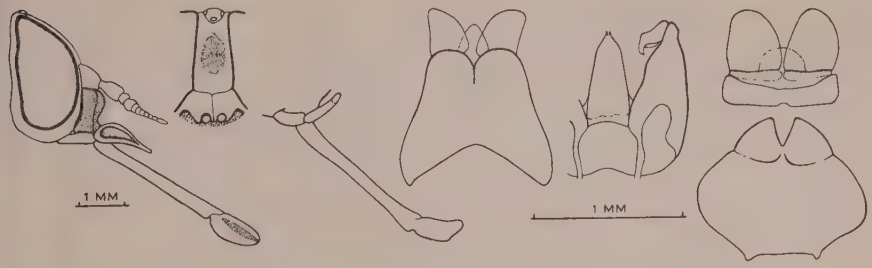


Fig. 32.—*Scaptia* (*Palimmecomyia*) *walkeri* (Newm.)

Distribution.—Australia: southern Queensland, New South Wales, South Australia, south-western Western Australia.

Ferguson (1926) accepted the genus as distinct, but it depends more on appearance than structural features, and I consider subgeneric status more appropriate. Both species are rare, and nothing is recorded of their habits.

Tribe PHILOLICHINI Mackerras, 1954

Style of ♂ simple, pointed, usually wider than in Scionini. Anterior gonopophyses of ♀ usually widely separated, the distal edge of the 8th sternite forming a characteristic, concave, chitinized projection, overlying which is a median, lightly chitinized, backwardly projecting tongue; the concave edge can sometimes be seen without dissection. Eyes bare, often distinctly separated in ♂. Ocelli absent or incomplete (except *Buplex*). Frons of ♀ wide (index 1 to 2.3), diverging, often partly, or sometimes wholly, shining. Face normal to strongly protuberant. Palpi (except *Phara*) small, with or without lateral bare concavity. Proboscis (except *Subpangonia*) rigid, varying in length from little more than head height to longer than body; normally with small, unexpanded labella. Cell R_5 open or closed; cell M_3 usually open; vein R_4 nearly always with well-developed appendix. Usually stoutly built, robust flies.

All the genera are African, with some extensions into other regions, and it is consequently appropriate to deal with them in a single series. I have followed the classification of Bequaert (1930), knowing that Oldroyd

will be revising the tribe, and that there will probably be changes and additions. Species marked with an asterisk in the following lists have been named by Mr. Oldroyd according to the present arrangement in the British Museum, which is still subject to review.

Genus BUPLEX Austen, 1920

Genotype: *Pangonia suavis* Loew, 1858, South Africa, by original designation.

Species examined.—suavis (Loew), ♀, det. Austen; *? albifacies* (Ric.), ♂ ♀, det. Oldroyd.

Female

Frons wide (index less than 2), entirely tomentose. Ocelli well developed, on a moderately developed ocellar tubercle. Subcallus normal, with fine hairs across upper portion. Face truncate, tomentose. Palpi less than one-third the length of the shaft of the proboscis, tapering apically, and with a lateral bare area or concavity. Proboscis less than twice head height, stiff, rather slender, with small unexpanded labella. Wing with cells R_5 and M_3 open. Hypopygium variable. *B. suavis* is undistinguished, except for the rather broad 8th sternite and strong, laterally expanded 9th tergite (seen somewhat end-on in Fig. 33*D*). In *B. ? albifacies*, the gonopophyses are unusually close together, 9th tergite wide and strong, and 10th tergite remarkably developed. The significance of these differences cannot be assessed on the material available.

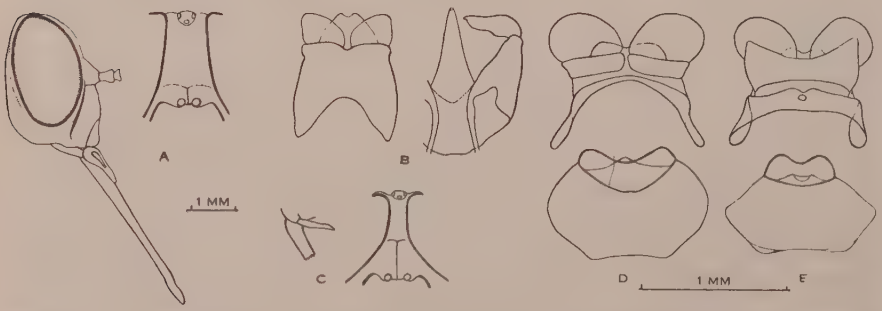


Fig. 33.—*A, D, Buplex suavis* (Loew) ♀; *B, C, E, B. ?albifacies* (Ric.), ♂ genitalia, palp and frons of ♂, ♀ genitalia.

Male

Similar to ♀. Eyes well separated and frons diverging, hairy (at least in *? albifacies*); palpi (Fig. 33*C*) subcylindrical, with a small dorsal bare area, rather like males of the *aurata* group of *Scaptia*. Fore tarsi without lappets. Hypopygium distinguished by the long, narrow aedeagus; style stout, as in *Philoliche*.

This genus is distinguished from its African relatives by possessing ocelli, and from *Scaptia* (*Pseudoscione*) by its bare eyes, wide frons, and tribal characters.

Distribution.—South Africa.

Genus OMMATIOSTERES Enderlein, 1922

Genotype: *Pangonia bifasciata* Enderlein, 1922, ? nec Wiedemann, 1821, South Africa, by original designation.

Species examined.—*bifasciata* (Wied.), ♀; *spiloptera* (Wied.), ♀; both det. Oldroyd.

My specimen of *Pangonia bifasciata* Wied. was identified by Mr. Oldroyd by comparison with the British Museum series, the correct determination of which was subsequently confirmed by comparison with Wiedemann's type. It is a *Philoliche,* with snout-like face, relatively long proboscis, cell R_5 narrowly open, and normal genitalia (Fig. 34*A* and *B*). It does not agree with Enderlein's definition of *Ommatiosteres,* so it seems evident that he misidentified his genotype.

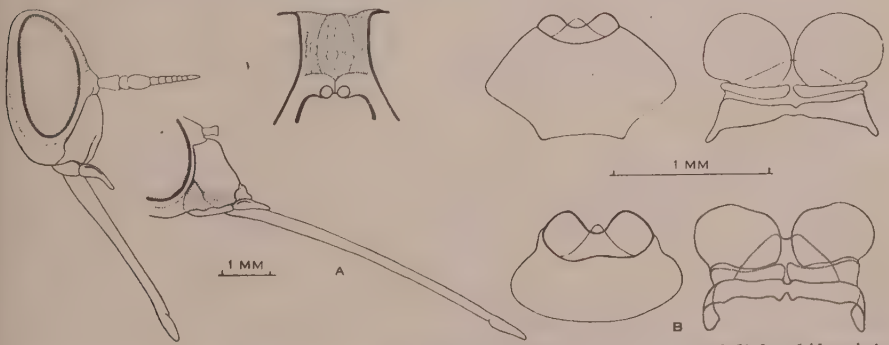


Fig. 34.—Top row, *Ommatiosteres spiloptera* (Wied.). *A, B, Philoliche bifasciata* (Wied.).

As represented by *O. spiloptera,* this group differs from *Buplex* in lacking ocelli, and in having a wider, wrinkled, somewhat shiny frons; from *Philoliche* in the truncate face and relatively short, stiff proboscis; and from *Stenophara* in the widely open cell R_5. The distal edge of the 8th sternite is relatively narrow, as in *Buplex ? albifacies.*

Distribution.—Most species South Africa; one from the Belgian Congo.

Genus PHILOLICHE Wiedemann, 1828

Genotype: *Tabanus rostratus* Linnaeus, 1764, South Africa, by designation of Coquillett, 1910.

Nuceria Walker, 1850. Type *Pangonia longirostris* Hardwicke, 1823, India, by designation of Coquillett, 1910. Discussed below.

Corizoneura Rondani, 1863. Type *Pangonia appendiculata* Macquart, 1838 (= *Tabanus aethiopicus* Thunberg, 1789), Africa, by designation of Coquillett, 1910.

Reduced to synonymy of *Nuceria* by Austen, 1920; I concur, from examination of genotype.

Stenophara Enderlein, 1922. Type *Pangonia longirostris* Hardwicke, 1823, India, by original designation.

Metaphara Enderlein, 1922. Type *Pangonia multifaria* Walker, 1848 (= *Pangonia gulosa* Wiedemann, 1828), South Africa, by original designation. Discussed below.

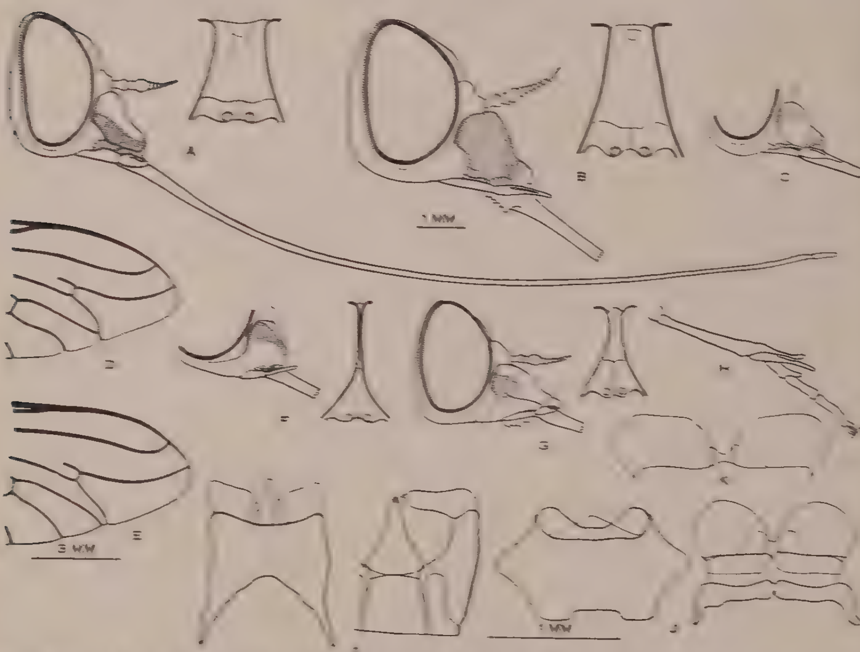


Fig. 35.—A, D, J, *Philoliche rostrata* (Linn.) ♀; B, E, K, *P. longirostris* (Hardw.) ♀; C, *P. distincta* (Ric.) ♀; F, I, *P. oldii* (Aust.) ♀; G, *P. gulosa* (Wied.) ♂; H, fore tarsus of *P. aethiopica* (Thunb.) ♀, showing lappets.

Species examined.—Ethiopian: *rostrata* (Linn.), ♀, det. Oldroyd; *aethiopica* (Thunb.),* ♂ ♀, det. Oldroyd; *gulosa* (Wied.), ♂, det. Oldroyd; *oldii* (Aust.), ♂ ♀, det. Austen; *distincta* (Ric.), ♀, det. Austen; sp. indet. (det. Austen as *aethiopica* var.), ♀. Oriental: *longirostris* (Hardw.), ♀, det. Oldroyd; sp. indet. (Assam), ♀. ? Australasian: sp. indet., ♂ (ex col. Bigot, labelled "New Zealand", but almost certainly not from that country).

This genus is the most characteristic development of the tribe in Africa, as *Fidena* is of Scionini in South America.

Female

Frons wide (index usually less than 2), more or less completely tomentose, with or without ocellar callus, usually without more than an

indication of a bare, shining central area. Subcallus projecting, tomentose, with or without hairs above or laterally. Face strongly projecting, snout-like, at least partly shining. Palpi variable; 2nd segment shorter than 1st, sometimes acorn-shaped, sometimes more elongate and slender, or somewhat flattened as in *Stenophara*; generally with a detectable dorso-lateral concavity or slit. There are intermediates connecting the palpal types illustrated. Proboscis slender, from little longer than head and thorax to twice length of whole body, with small, unexpanded labella. Wing with cell R_5 variable, usually more or less markedly narrowed at margin, or closed and short-petiolate; cell M_3 widely open. Hypopygium with 8th sternite wide, its distal rolled edge narrow to medium, occasionally quite wide; 9th tergite strong, but more or less narrowed in middle; 10th tergite little if at all chitinized; cerci rounded or truncate distally; caudal ends of spermathecal ducts slender.

Male

Eyes sometimes meeting in mid-line, sometimes quite well separated by a diverging, hairy frons; ocellar tubercle well developed. Palpi variable, sometimes resembling ♀, sometimes more slender and rod-like. Wings as in ♀, but cell R_5 may be less constricted or shorter-petiolate at margin. Fore tarsi with or without long, projecting lappets. Hypopygium with aedeagus large, extending distally beyond level of tip of coxite; flagella strong; style stout.

Distribution.—? Palaearctic: Two species recorded doubtfully by Kröber (1939). Ethiopian: Widely distributed over South, Equatorial, and East Africa as far north as Eritrea. Oriental: India; Ceylon. Australasian: Timor; Amboina; New Caledonia.

Oldroyd (1947) doubted whether *Nuceria* could be maintained as generically distinct from *Philoliche*. The two genotypes are very similar in the characters of the head and genitalia of the female, and both are described as having lappets on the fore tarsi of the male. They differ in the shape of the palpi, closure of cell R_5 (Fig. 35*D*, *E*), and in the cerci, which are rounded in *rostrata* and other African species examined, truncate in *longirostris* and the species from Assam. These differences are minor, and I feel that *Nuceria* must therefore fall to synonymy.

This does not necessarily mean that *Philoliche* cannot be further subdivided. There may, for example, be a division between species (*rostrata, aethiopica, longirostris*, etc.) that possess lappets on the fore tarsi of the male and those (*oldii, gulosa*, etc.) that lack them. I have not, however, found any significant differences between the genitalia of the species examined, and there appears to be a gradation in other characters, leading from the first group to the second, and from the second to *Stenophara*.

Metaphara was proposed by Enderlein in his silviine tribe Scarphiini. Mr. Oldroyd was kind enough to lend me a male of *Pangonia gulosa* Wied.,

which, he informed me, agreed well with the type of *Pangonia multifaria* Walk. It is clearly a *Philoliche*, being unusual only in the well-separated eyes (Fig. 35*G*); the genitalia are exactly like those of *P. oldii* (Fig. 35*I*). It is difficult to understand how Enderlein came to describe the 3rd antennal segment as 5-annulate.

The feeding habits of the females with extraordinarily long proboscis have excited considerable curiosity, particularly as the piercing parts are very much shorter than the labium (8 mm as against 30 in *P. longirostris*, according to Mitter (1918)). There appear to be two distinct methods of obtaining food. Sen (1931) has described *P. longirostris* feeding in the deep flowers of *Roscoea purpurea*, hovering with labium outstretched, like a sphingid moth, and, he believed, scooping up the nectar with its labella. Its manner of obtaining a blood meal is quite different. Mitter (1918) observed it to hover close to its host, detach the labium from the stylets, and make sudden darts, thrusting with the stylets. If undisturbed, it alighted, raised itself on its hind legs, and worked through the skin with the piercing parts, which were held perpendicularly to the long axis of the body. The labium played no part in sucking, and was held back between the legs or to one side.

This remarkable division of function may be general, but would not be easy to detect in species with normal mouth-parts and little discrepancy in length between labium and stylets.

Genus STENOPHARA Enderlein, 1922

Genotype: *Pangonia zonata* Walker, 1871, Arabia; Somaliland; by original designation.

Species examined.—lautissima (Aust.), ♂ ♀, det. Oldroyd; *beckeri* (Bezzi), ♀, det. Austen; *conjuncta* (Walk.),* ♂ ♀ ; *alboatra* (Walk.),* ♀ ; *magrettii* (Bezzi), ♂ ♀ ; all det. Oldroyd.

This group is of doubtful validity, in that it tends to grade into the section of *Philoliche* without lappets on the fore tarsi of the male. It may be defined broadly as follows.

Female

Face not as protuberant as in *Philoliche*, extensively shining. Third antennal segment shorter and thicker than usual in *Philoliche*. Palpi flattened and tapering, with inconspicuous dorsolateral slit. Proboscis short, less than twice head height, relatively strong and stiff. Wing with cell R_5 long-petiolate; vein R_5 relatively strongly curved, and sometimes with a stump-vein (Fig. 36*B*); cell M_3 widely open. Eighth sternite with strongly projecting gonopophyses.

Male

Eyes contiguous or distinctly separated. Ocellar tubercle not visible. Palpi slender, rod-like, or gently tapering. Fore tarsi without lappets. Aedeagus small and short, not reaching level of tips of coxites.

Distribution.—Ethiopian: South Africa; Angola; Belgian Congo; East Africa north to Eritrea. Arabia. ? Palaearctic: ? Persia and Caucasus.

S. lautissima and *S. beckeri* are strongly built but relatively long bodied species, with short proboscis, and distinctive general appearance. *S. conjuncta* and *S. alboatra* agree with them structurally, but the body

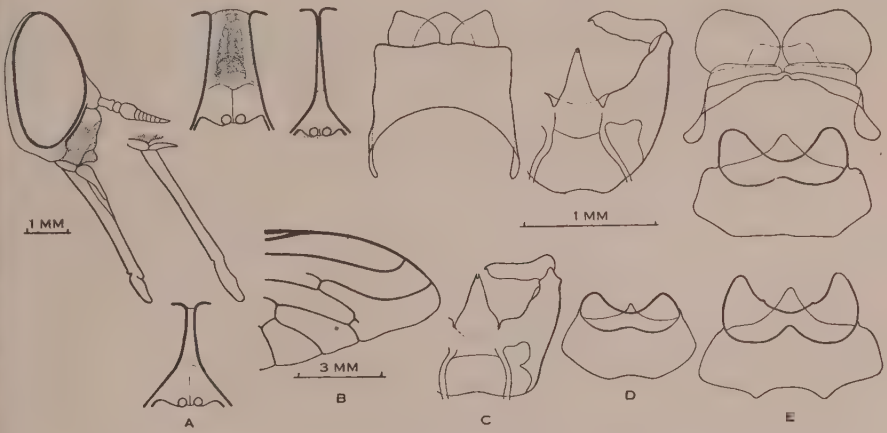


Fig. 36.—Top series: *Stenophara lautissima* (Aust.). Lower series: *A, B, S. conjuncta* (Walk.), head of ♂, wing of ♀; *C, D, S. magrettii* (Bezzi); *E. S. beckeri* (Bezzi).

is more rounded, and the proboscis distinctly longer and more slender. *S. magrettii* also has a relatively slender proboscis, and is intermediate between *Stenophara* and *Philoliche* in so many respects, including the genitalia (Fig. 36*C, D*), that it could be placed with almost equal propriety in either. It is not possible to comment further without having seen the genotype.

Genus DORCALOEMUS Austen, 1910

Genotype: *Pangonia compacta* Austen, 1908, East Africa, by original designation.

Species examined.—compactus (Aust.), ♀, det. Austen; *fodiens* Aust., ♂ ♀, det. Austen; *woosnami* Aust., ♂ ♀, det. Austen.

This genus is closely related to *Stenophara,* with which it agrees in the short proboscis, flat palpi, long-petiolate cell R_5, with strongly curved vein R_5 showing indications of a stump, shape of 8th sternite in the ♀, and the very small aedeagus in the ♂. It differs in the development of a relatively well-defined "callus", possibly in the slender style of the ♂ hypopygium, in the more broadly rounded apex of the wing (Fig. 37*F*), and in the closed cell M_3. This last appears to be as constant here as it is

in the South American *Scione*, and the genus seems equally worthy of recognition.

Distribution.—Belgian Congo (Katanga) : East Africa from Southern Rhodesia to Abyssinia.

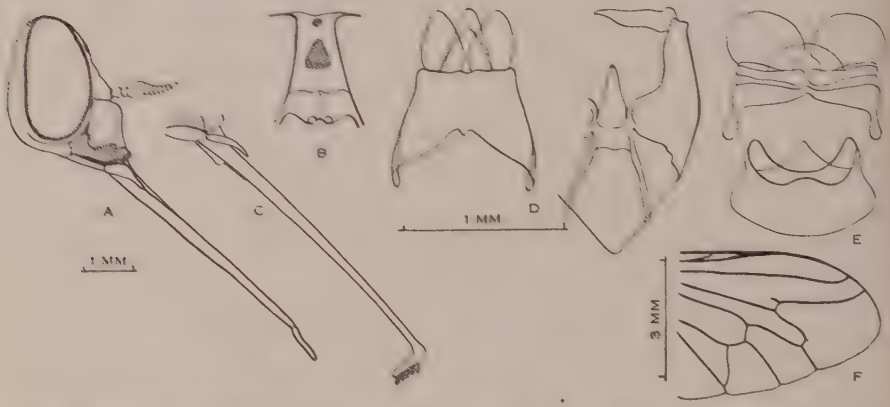


Fig. 37.—*A, B, Porcaloemus compactus* (Aust.) ♀ ; *C, D. woosnami* Aust. ♂ ; *D, E, F, D. fodiens* Aust., ♂ and ♀ genitalia, wing of ♀.

Genus PHARA Walker, 1850

Genotype: *Pangonia melanopyga* Wiedemann, 1819, South Africa, by designation of Coquillett, 1910.

Cadicera Macquart, 1855. Originally monotypic for *Cadicera rubramarginata* Macquart, 1855, South Africa. Synonymy by Austen, 1920.

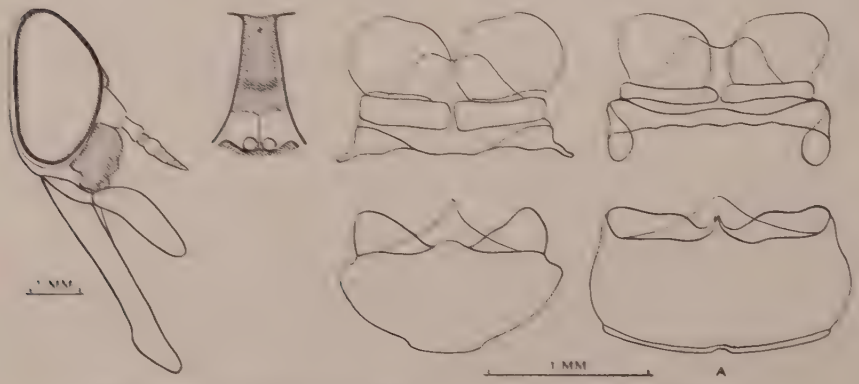


Fig. 38.—*Phara biclausa* (Wied.). *A, P. chrysostigma* (Wied.).

Species examined.—*rubramarginata* (Macq.),* ♀, det. Oldroyd; *biclausa* (Loew), ♀, det. Austen; *chrysostigma* (Wied.),* ♀, det. Oldroyd.

Female

This genus stands rather strikingly apart from the others, though it shows some indications of affinity with *Stenophara.* The body is broad and flat, the face bulging, the proboscis short, stiff, and stout, with well-developed, firm labella, and the palpi large and swollen. The frons is relatively narrow (index greater than 2), the 3rd antennal segment somewhat thickened basally, and the genitalia are peculiar. The gonopophyses are separated by a median band of delicate chitin, and the 9th tergite in two of the three species is so attenuated in the middle as to be, in effect, divided into a lateral plate on each side.

Distribution.—South Africa; east Africa as far north as Zanzibar.

Genus SUBPANGONIA Surcouf, 1908

Genotype: originally monotypic for *Subpangonia gravoti* Surcouf, 1908, French Congo.

Species examined.—gravoti Surc., ♀, det. Oldroyd.

Female

Related to more generalized *Stenophara,* but distinguished by a flatter head, narrower, parallel-sided frons, truncate face, rudimentary appendix to vein R_4 (at least in the specimen examined), and especially by the remarkable modification of the proboscis. The labella are long and soft,

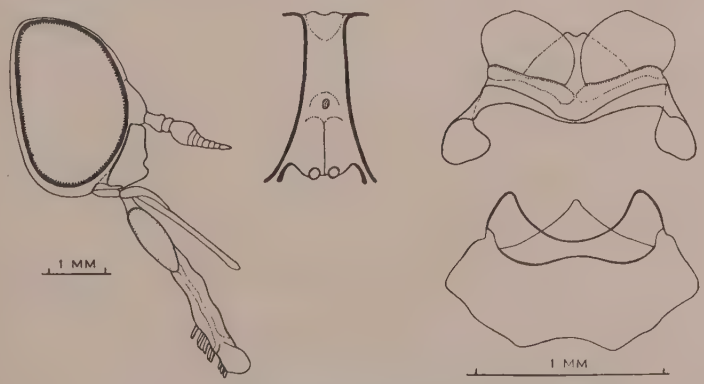


Fig. 39.—*Subpangonia gravoti* Surc.

and are armed with a series of elongate pseudotracheal processes, which can be seen quite easily from the side. This character is not unique, as noted by Austen (1912), in that similar, but smaller, processes can sometimes be seen in specimens of *Stenophara* and *Dorcaloemus,* in which the labella happen to be sufficiently separated to see between them (Fig. 37*C*). The 9th tergite is expanded laterally and attenuated in the middle, much as in *Phara,* but otherwise the genitalia are not distinctive.

Distribution.—The three known species appear to be confined to the rain-forests of the West African subregion.

X. ACKNOWLEDGMENTS

I am indebted to the Council of the Linnean Society of New South Wales and to the Director of the Commonwealth Institute of Entomology, London, for permission to use the illustrations which have been assembled to make up Figure 3 of the present paper.

XI. REFERENCES

AUSTEN, E. E. (1912).—New African Tabanidae. I. *Bull. ent. Res.* **3**: 113-36.

AUSTEN, E. E. (1920).—Notes on the nomenclature of certain African Tabanidae (subfamily Pangoniinae), with descriptions of a new genus and new species. *Bull. ent. Res.* **11**: 139-52.

BEQUAERT, J. (1924).—Notes upon Surcouf's treatment of the Tabanidae in the Genera Insectorum and upon Enderlein's proposed new classification of this family. *Psyche Camb. Mass.* **31**: 24-40.

BEQUAERT, J. (1930).—"The African Republic of Liberia and the Belgian Congo." Entomology: Tabanidae. Vol. 2. pp. 858-971. (Harvard Univ. Press.)

BORGMEIER, T. (1933).—A proposito da nomenclatura dos Tabanidae da regiae neotropica. *Rev. Ent. Rio de J.* **3**: 286-303.

BOUVIER, G. (1945).—Note sur l'armature génitale des Tabanides. *Mitt. schweiz. ent. Ges.* **18** (2): 57-61.

BRENNAN, J. M. (1935).—The Pangoniinae of Nearctic America (Diptera: Tabanidae). *Kans. Univ. Sci. Bull.* **22**: 249-401.

COLE, F. R. (1927).—A study of the terminal abdominal structures of male Diptera (two-winged flies). *Proc. Calif. Acad. Sci.* **16**: 397-499.

COQUILLETT, D. W. (1910).—The type-species of the North American genera of Diptera. *Proc. U.S. Nat. Mus.* **37**: 499-647.

ENDERLEIN, G. (1922).—Ein neues Tabanidensystem. *Mitt. zool. Mus. Berl.* **10** (2): 333-51.

ENDERLEIN, G. (1925).—Studien an blutsaugenden Insekten. I. Grundlagen eines neuen Systems der Tabaniden. *Mitt. zool. Mus. Berl.* **11** (2): 253-409.

ENDERLEIN, G. (1932).—Einige neue paläarktische Tabaniden (Dipt.). *Mitt. dtsch. ent. Ges.* **3**: 63-4.

ENGLISH, K. M. I. (1952).—Notes on the morphology and biology of *Ectenopsis vulpecula* Wied. var. *angusta* Macq. (Diptera, Tabanidae, Pangoniinae). *Proc. Linn. Soc. N.S.W.* **77**: 270-4.

ENGLISH, K. M. I. (1955).—Notes on the morphology and biology of *Scaptia violacea* Tayl. and a new species of *Scaptia* (Diptera, Tabanidae). *Proc. Linn. Soc. N.S.W.* **79**: 219-29.

FAIRCHILD, G. B. (1941).—Notes on Tabanidae (Dipt.) from Panama. VI. The genus *Fidena* Walker. *Ann. ent. Soc. Amer.* **34**: 639-46.

FAIRCHILD, G. B. (1942a).—Notes on Tabanidae (Dipt.) from Panama. VIII. The genera *Pityocera*, *Scione* and *Esenbeckia*. *Ann. ent. Soc. Amer.* **35**: 183-99.

FAIRCHILD, G. B. (1942b).—Notes on Tabanidae (Dipt.) from Panama. X. The genus *Tabanus* Linn., and resume of the Tabanidae of Panama. *Ann. ent. Soc. Amer.* **35**: 441-74.

FAIRCHILD, G. B. (1950).—The generic names for Tabanidae (Diptera) proposed by Adolfo Lutz. *Psyche Camb. Mass.* **57**: 117-27.

FAIRCHILD, G. B. (1951).—Descriptions and notes on Neotropical Tabanidae. *Ann. ent. Soc. Amer.* **44**: 441-62.

FERGUSON, E. W. (1915).—Descriptions of new Australian blood-sucking flies belonging to the family Leptidae. *J. Roy. Soc. N.S.W.* **49**: 233-43.

FERGUSON, E. W. (1921).—New Australian Tabanidae, with notes on previously described species. *Proc. Roy. Soc. Vict.* **33**: 1-29.

FERGUSON, E. W. (1924).—Notes on the nomenclature of Australian Tabanidae: subfamily Pangoniinae. *Bull. ent. Res.* 14: 251-63.

FERGUSON, E. W. (1926).—Additional notes on the nomenclature of Australian Tabanidae. *Bull. ent. Res.* 16: 293-306.

FERGUSON, E. W., and HILL, G. F. (1922).—Notes on Australian Tabanidae. Part ii. *Proc. Linn. Soc. N.S.W.* 47: 245-65.

FULLER, M. E. (1936).—Notes on the biology of *Scaptia auriflua* Don. (Diptera, Tabanidae). *Proc. Linn. Soc. N.S.W.* 61: 1-9.

FULLER, M. E. (1937).—Notes on the biology of *Tabanus froggatti*, *T. gentilis*, and *T. neobasalis* (Diptera). *Proc. Linn. Soc. N.S.W.* 62: 217-29.

HACK, W. H. (1953).—Segunda contribucion al estudio de los Tabanidos Argentinos (Diptera). *Ann. Inst. Med. Region. Tucuman* 3: 339-47.

HARDY, G. H. (1944).—Miscellaneous notes on Australian Diptera. X. Distribution, classification and the *Tabanus posticus*-group. *Proc. Linn. Soc. N.S.W.* 69: 76-86.

HENNIG, W. (1952).—"Die Larvenformen der Dipteren." Vol. 3. 628 pp. (Akademie-Verlag: Berlin.)

HILL, G. F. (1921).—The bionomics of *Tabanus aprepes* and other Australian Tabanidae. *Bull. ent. Res.* 12: 41-62.

KROBER, O. (1925).—Tabanidae. In Lindner, E.: "Die Fliegen der palaearktischen Region." Vol. 19. pp. 1-146. (Stuttgart.)

KROBER, O. (1930*a*).—Die Stenotabaninae und die Lepidoselaginae Südamerikas. *Encycl. ent.* B II Dipt. 5: 101-54.

KROBER, O. (1930*b*).—"Tabanidae. Diptera of Patagonia and South Chile." V. Fasc. 2. pp. 106-61. (British Museum (Nat. Hist.): London.)

KROBER, O. (1932).—Bemerkungen über die Systematik der neotropischen Tabaniden, nebst Bestimmungstabelle der Subfamilien und Gattungen (Dipt.). *Rev. Ent. Rio de J.* 2: 185-202.

KROBER, O. (1934).—Catalogo dos Tabanidae da America do Sul e Centrale, incluindo o Mexico e as Antilhas. *Rev. Ent. Rio de J.* 4: 222-76, 291-333.

KROBER, O. (1939).—Katalog der palaearktischen Tabaniden nebst Bestimmungstabellen und Zusätzen zu einzelnen Arten sowie Neubeschreibungen. *Acta Inst. Zool. Univ. Athen.* 2: 57-245.

LOEW, H. (1860).—"Dipterenfaunas Süd-Afrikas." (Berlin.)

LUTZ, A. (1905).—Beiträge zur Kenntnis der brasilianischen Tabaniden. Rev. Soc. sci. S. Paulo No. 1: 17-32.

LUTZ, A. (1909).—Tabaniden Brasiliens und einiger Nachbarstaaten. *Zool. Jb.* 1909 Suppl. 10: 619-92.

LUTZ, A. (1913).—Sobre a systematica das Tabanideos sub-familia Tabaninae. Brazil-Med. No. 45: 7 pp.

MACKERRAS, I. M. (1954).—The classification and distribution of Tabanidae (Diptera). I. *Aust. J. Zool.* 2: 431-54.

MACKERRAS, I. M. (1955).—The classification and distribution of Tabanidae (Diptera). III. Subfamilies Scepsidinae and Chrysopinae. *Aust. J. Zool.* 3: (in press).

MACKERRAS, I. M., and FULLER, M. E. (1942).—The genus *Pelecorhynchus* (Diptera, Tabanoidea). *Proc. Linn. Soc. N.S.W.* 67: 9-76.

MALLOCH, J. R. (1932).—"Rhagionidae. Diptera of Patagonia and South Chile." V. Fasc. 3: pp. 199-235. (British Museum (Nat. Hist.): London.)

MARCHAND, W. (1920).—The early stages of Tabanidae (horseflies). Monogr. Rockefeller Inst. Med. Res. Vol. 13: 203 pp. (New York.)

MARINO, M. T. P. (1951).—I Pangonini (Diptera, Tabanidae) italiani e loro rapporti con la fauna paleartica. *Redia* 36: 277-90.

MITTER, J. L. (1918).—Note on the method of feeding of *Corizoneura* (*Pangonia*) *longirostris* Hardwick, with a description of the mouth parts. *Indian J. med. Res.* 5: 523-8.

NICHOLSON, A. J. (1927).—A new theory of mimicry in insects. *Aust. Zool.* 5: 10-104.

OLDROYD, H. (1947).—The Diptera of the Territory of New Guinea. XIV. Family Tabanidae. Part II. Pangoniinae, except the genus *Chrysops*. *Proc. Linn. Soc. N.S.W.* 72: 125-42.

OLDROYD, H. (1949).—The Diptera of the Territory of New Guinea. XIV. Family Tabanidae. Part iii. Tabaninae. *Proc. Linn. Soc. N.S.W.* 73: 304-61.

OVAZZA, M., and TAUFFLIEB, R. (1954).—Les genitalia femelles des Tabanides et leur importance en systématique. *Ann. Parasit. hum. comp.* 29: 250-64.

PEREIRA BARRETTO, M. (1946).—Estudos sôbre Tabânidas brasileiros. I. Morfologia externa do *Tabanus* (*Poiciloderas*) *quadripunctatus* Fab. *Ann. Fac. Med. S. Paulo* 22: 113-49.

PEREIRA BARRETTO, M. (1950).—Estudos sôbre Tabânidas brasileiros. XI. Sôbre a validade nomenclatural dos nomes genéricos em "Colleção de Tabânidas, Instituto Oswaldo Cruz em Manguinhos, Rio de Janiero, 1909" (Diptera, Tabanidae). *Pap. Dep. Zool. Sec. Agric. S. Paulo* 9: 61-8.

PHILIP, C. B. (1941*a*).—Comments on the supra-specific categories of Nearctic Tabanidae (Diptera). *Canad. Ent.* 73: 2-14.

PHILIP, C. B. (1941*b*).—Notes on Nearctic Pangoniinae (Diptera, Tabanidae). *Proc. ent. Soc. Wash.* 43: 113-30.

PHILIP, C. B. (1943).—New Neotropical Tabanidae (Diptera). *J. N.Y. ent. Soc.* 51: 111-16.

PHILIP, C. B. (1947).—A catalog of the blood-sucking fly family Tabanidae (horseflies and deerflies) of the Nearctic region north of Mexico. *Amer. Midl. Nat.* 37: 257-324.

PHILIP, C. B. (1954).—New North American Tabanidae (Diptera). IV. *Zophina* new genus for "*Apatolestes*" *eiseni* Townsend from lower California. *Pan-Pacif. Ent.* 30: 53-6.

PHILIPPI, R. A. (1865).—Aufzählung der chilenischen Dipteren. *Verh. zool.-bot. Ges. Wien* 15: 595-782.

RICARDO, G. K. (1915).—Notes on the Tabanidae of the Australian region. (Continuation.) *Ann. Mag. nat. Hist.* (8) 16: 16-40.

SCHUURMANS STEKHOVEN, J. H. (1926).—The bloodsucking Arthropods of the Dutch East Indian Archipelago. VII. The tabanids of the Dutch East Indian Archipelago. *Treubia* 6: suppl. 551 pp.

SCHUURMANS STEKHOVEN, J. H. (1932).—Tabanidae. Résultats scientifiques du voyage aux Indes Orientales Neerlandaises de LL. AA. RR. le Prince et la Princesse Léopold de Belgique. *Mém. Mus. hist. nat. Belg.* (hors série), T.4, fasc. 7: 11-16.

SEGUY, E. (1926).—"Faune de France." ch. 13. Diptères (Brachycères). Tabanidae pp. 119-57. (Paris: Lechevelier.)

SEGUY, E. (1929).—Une Pangonie nouvelle de Maroc. *Encycl. ent.* B II Dipt. 5: 100.

SEN, S. K. (1931).—Notes on the bionomics and anatomy of *Corizoneura longirostris* Hardwicke (Diptera: Family Tabanidae; subfamily Pangoniinae). *Indian J. vet. Sci.* 1: 24-8.

STEYSKAL, G. C. (1953).—A suggested classification of the lower Brachycerous Diptera. *Ann. ent. Soc. Amer.* 46: 237-42.

STONE, A. (1953).—New tabanid flies of the tribe Merycomyiini. *J. Wash. Acad. Sci.* 43: 255-8.

SURCOUF, J. M. R. (1921).—Diptera. Fam. Tabanidae. Wytsman's *Genera Insectorum* Fasc. 175: 182 pp.

SZILADY, Z. (1923).—New or little-known horseflies (Tabanidae). *Biol. Hung.* 1: 1-39.

SZILADY, Z. (1926).—Kritische Bemerkungen über Enderleins Tabaniden-system. *Zool. Anz.* 66: 325-8.

List of Genera